MANUAL ASYMMETRIES, HANDEDNESS AND MOTOR PERFORMANCE

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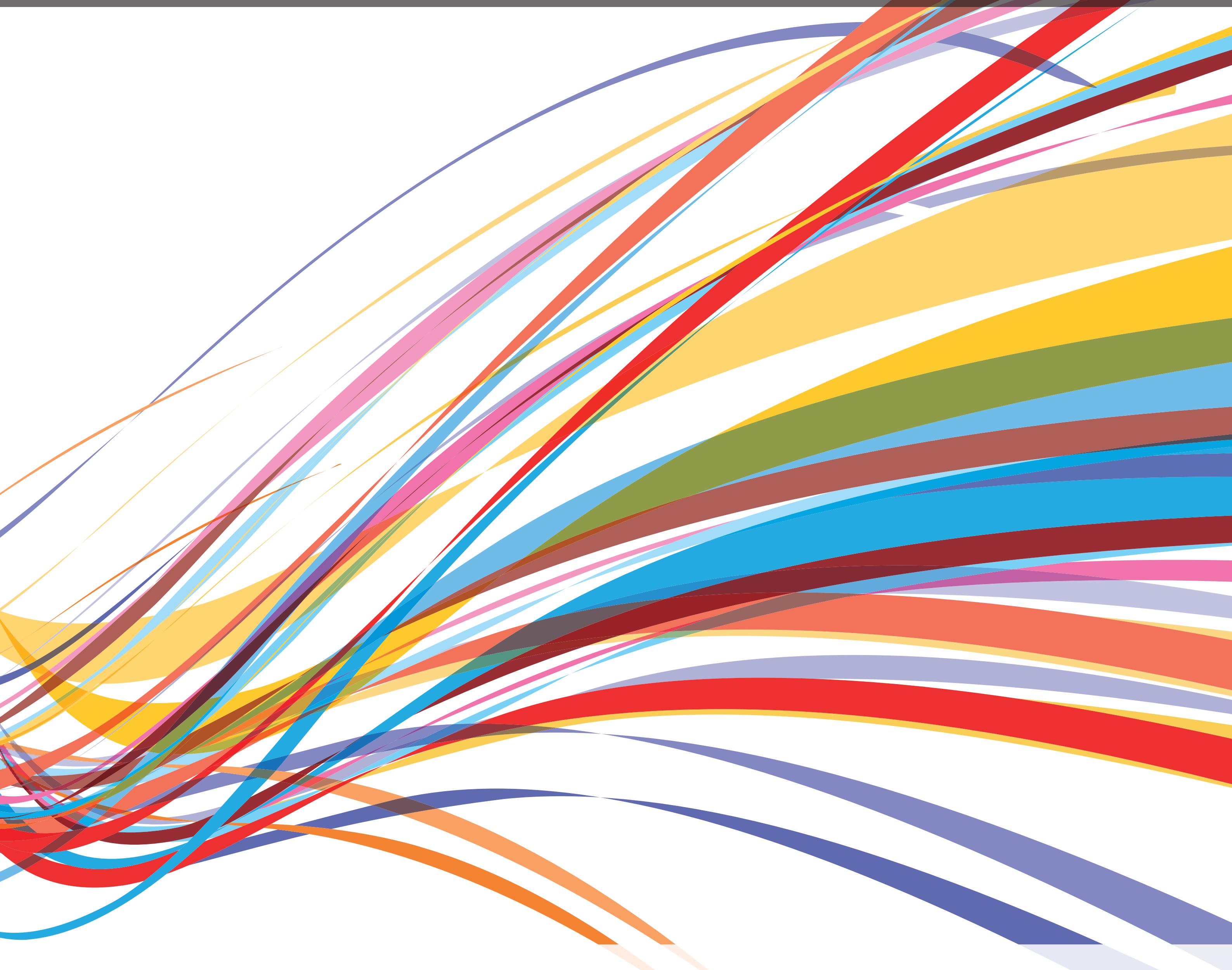
PUBLISHED IN: Frontiers in Psychology



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ISSN 1664-8714
ISBN 978-2-88919-863-4
DOI 10.3389/978-2-88919-863-4

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MANUAL ASYMMETRIES, HANDEDNESS AND MOTOR PERFORMANCE

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The performance of most tasks with one hand, typically the right, is a uniquely human characteristic. Not only do people prefer to use one hand rather than the other, but also they usually perform tasks faster and more accurately with this hand. The study of manual asymmetries and what such performance differences between the two hands reveal about brain organization and motor function has been a topic of considerable research over the last several decades. The aim of this Research Topic is to review and further explore the origins of manual asymmetries and their relationship to handedness, unimanual and bimanual motor performance, and brain function.

The articles included here involve original research conducted in humans or non-human models species, as well as theoretical perspectives, review articles, and meta-analyses.

Citation: Bryden, P., Mason, A. H., Gonzalez, C. L. R., eds. (2016). Manual Asymmetries, Handedness and Motor Performance. Lausanne: Frontiers Media. doi: 10.3389/978-2-88919-863-4

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frontiers in PSYCHOLOGY

REVIEW ARTICLE
published: 08 October 2014
doi: 10.3389/fpsyg.2014.01092

Convergent models of handedness and brain lateralization

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The pervasive nature of handedness across human history and cultures is a salient consequence of brain lateralization. This paper presents evidence that provides a structure for understanding the motor control processes that give rise to handedness. According to the Dynamic Dominance Model, the left hemisphere (in right handers) is proficient for processes that predict the effects of body and environmental dynamics, while the right hemisphere is proficient at impedance control processes that can minimize potential errors when faced with unexpected mechanical conditions, and can achieve accurate steady-state positions. This model can be viewed as a motor component for the paradigm of brain lateralization that has been proposed by Rogers et al. (MacNeilage et al., 2009) that is based upon evidence from a wide range of behaviors across many vertebrate species. Rogers proposed a left-hemisphere specialization for well-established patterns of behavior performed in familiar environmental conditions, and a right hemisphere specialization for responding to unforeseen environmental events. The dynamic dominance hypothesis provides a framework for understanding the biology of motor lateralization that is consistent with Roger's paradigm of brain lateralization.

Keywords: handedness, brain lateralization, laterality, motor activity, manual asymmetry, motor lateralization, motor neurons

A GENERALIZED MODEL OF VERTEBRATE BRAIN LATERALIZATION

The division of labor between the two sides of the brain is a basic organizational feature of the vertebrate nervous system that arose in evolution even before the appearance of vertebrates (MacNeilage et al., 2009). According to the work of Rogers and colleagues, a single organizing principle might account for the large array of emotional, language, perceptual, and cognitive asymmetries that have been described across a range of vertebrate animals, including humans. They proposed that the left hemisphere has become specialized for control of well-established patterns of behavior, performed under familiar environmental circumstances, while the right hemisphere has become specialized for detecting and responding to unexpected stimuli in the environment. This elegant hypothesis was derived through seeking fundamental principles from a wide variety of experimental and natural observations of behavior. It is an example of a parsimonious principle that can account for a large range of observable behaviors, a foundation of the scientific process (Brody, 1994). Rogers further hypothesized that separating neural circuits across the hemispheres might reduce interference between potentially competing processes, thus allowing more efficient behavior. In a test of this hypothesis, Rogers and colleagues compared visual processing behaviors in groups of chicks with and without lateralized visual systems, controlled by exposing the embryo to different light regimes (Rogers et al., 2004; Vallortigara and Rogers, 2005). After hatching, the two groups of chicks were tested on a dual task, which required a normally right hemisphere process, scanning for predators, and a normally left hemisphere process, sorting food grains from pebbles. The results indicated that both groups performed each isolated task well, but only the lateralized chicks could effectively carry out the two tasks simultaneously. Thus, a single integrated behavior involving sorting food and scanning the environment is accomplished by recruiting two neural processes, across the two hemispheres. This both supports the hypothesis that neural lateralization imparts behavioral efficiency through separation of parallel neural processes, and suggests how lateralization might have contributed to natural selection in the evolutionary process. Recent research examining motor control differences between the dominant and non-dominant arms suggests that Roger's hypothesis might also explain handedness. That is, the left hemisphere (in right handers) might be specialized for controlling movements through predictive mechanisms that are most effective under consistent and stable mechanical conditions, while the right hemisphere might be specialized for impedance control, which imparts stability when mechanical conditions are unpredictable, or when stabilizing steady state position at the end of a movement.

THE DYNAMIC DOMINANCE HYPOTHESIS PROVIDES A FRAMEWORK FOR UNDERSTANDING HANDEDNESS WITHIN ROGER'S HYPOTHESIS

Over the past decade, our laboratory has developed a model of motor lateralization (Sainburg, 2002, 2005; Mutha et al., 2012, 2013) that can be viewed as a motor control analog for the model of brain lateralization developed and elaborated by Rogers and colleagues. This model is based on fundamental principles of control theory that account for a range of experimental findings in different tasks and task conditions. The dynamic dominance hypothesis of motor lateralization proposes that the left hemisphere (in right-handers) is specialized for processes that account for predictable dynamic conditions, in order to specify movements that are mechanically efficient, and have precise trajectories. In contrast, the right hemisphere (in right-handers) is specialized for impedance control mechanisms that ensure positional and velocity stabilization in the face of unpredictable mechanical events and conditions, and accuracy and stability of steady state postures. The former process assures mechanical efficiency and trajectory specificity under predictable conditions, while the latter imparts robustness under unpredictable conditions, as well as postural stability. Through studies in stroke patients with specific unilateral brain lesions, we have provided evidence that both processes contribute to control of each arm. However, the hemisphere contralateral to a given arm imparts the greatest influence to that arm's performance. In terms of Roger's hypothesis, the right hemisphere is specialized for a system that ensures stability and rapid online responses to unexpected stimuli in the internal and external environments, while the left hemisphere exploits predictive processes to assure trajectory precision and mechanical efficiency when conditions are consistent and predictable.

HYBRIDIZATION OF PREDICTIVE AND IMPEDANCE MECHANISMS ALLOWS EFFICIENT AND ROBUST CONTROL OF MOVEMENTS

Energy conservation has clearly played a significant role in the process of human evolution, contributing to our tendency to exploit coordination patterns that are energy efficient (Alexander, 1997; Nishii and Taniai, 2009). Predictive mechanisms can be used in order to minimize costs, such as energy and smoothness, when environmental conditions are predictable. Thus, optimality is an important principle for predictive control (Todorov, 2004). However, because environmental conditions are often unpredictable, impedance control through modulation of feedback gains is also an important component of biological movements (Scott, 2004; Mutha et al., 2008; Omrani et al., 2013). Indeed, from a mechanical perspective, the world can be very unstable and unpredictable. For example, inertial interactions while riding in a vehicle and holding or reaching for a cup of coffee can be quite large when changes in acceleration are not anticipated. Similarly, slicing an irregular shaped piece of fruit or vegetable can be unstable because it can slip or rock with force components applied by a knife. It should also be stressed that one's own motor commands can introduce unanticipated errors in intended movements, due to errors in prediction, and noise in central processes that might include erroneous sensory estimates (Faisal and Wolpert, 2009). Thus, in addition to predictive mechanisms that can produce smooth and efficient coordination patterns, impedance mechanisms can assure stability in the face of unexpected external and internal conditions, and can assure steady state positions at the end of motion.

Predictive control mechanisms can be used to optimize a combination of kinematic and dynamic costs of movement (Hogan and Sternad, 2009; Yadav and Sainburg, 2011). Examples of component costs that have been proposed in the literature include Movement Smoothness, Mean Squared Torque, Peak Work, Muscle Energy and Final Position Variability (Osu et al., 1997; Kawato and Wolpert, 1998; Kawato, 1999; Harris and Wolpert, 2006). However, predictive control based on such optimization principles, whether implemented through open loop or optimal feedback control schemes (Todorov, 2005), is not robust to unanticipated changes in task conditions. In addition, achieving stable final positions through such mechanisms can be sensitive to internally generated prediction errors and neural noise. In fact, in a recent series of experiments, Scheidt and Ghez (Ghez et al., 2007; Scheidt and Ghez, 2007) demonstrated independent mechanisms for controlling limb trajectory and final position during reaching movements. According to their findings, trajectory control was generated largely by predictive mechanisms, and final position stability was achieved largely through mechanisms similar to impedance control.

How can impedance control counter unanticipated perturbations and stabilize final positions? Mechanical impedance includes 3 components that vary with acceleration, velocity, and position. While the first is dependent on inertia, and cannot actively be modulated, the effective stiffness-like and viscous-like behavior of the limb can be neurally modulated (Shadmehr and Arbib, 1992). The mechanisms through which impedance modulation can occur include muscle co-activation (Gomi and Kawato, 1997; Burdet et al., 2001; Osu et al., 2009), as well as modulation of proprioceptive reflex gains and thresholds (Mutha et al., 2008; Pruszynski et al., 2011). It has previously been demonstrated that impedance mechanisms can provide stability of the trajectory and final position during the initial phases of motor learning (Takahashi et al., 2001), or when environmental conditions are unstable or unpredictable (Milner and Franklin, 2005; Burdet et al., 2006). Schabowsky et al. (2007) and Duff and Sainburg (2007) have shown that the non-dominant arm tends to rely on impedance control for adaptation, even when conditions are predictable, whereas, the dominant arm tends to rely on predictive mechanisms to a greater extent. However, impedance control mechanisms cannot be used to optimize factors such as energy expenditure, and thus can result in high energetic costs. This is consistent with the finding that the non-dominant arm, which relies on such control, tends to perform movements with higher energetic cost than the dominant arm (Bagesteiro and Sainburg, 2002) Thus, each control scheme offers advantages, which can counter the disadvantages of the alternate control scheme.

The hybridization of predictive and impedance control mechanisms for smooth and energetically efficient movements that can resist unpredictable mechanical interactions has previously been well-established. For example, Takahashi et al. (2001) exposed subjects to two alternative force fields imposed by a robotic manipulandum (see **Figure 1A**), while they reached toward targets with the dominant arm. The force fields were proportional to velocity and directed perpendicular to the targeted movements, tending to impose perpendicular deviations in the movement paths. Subjects were either exposed to a consistent field, or a field that varied in magnitude from trial to trial, but had the same mean amplitude as the consistent field. When initially exposed to the consistent field, subjects showed large errors in the direction of the field (**Figure 1B**, negative peak), yet over practice were able to eliminate these errors. When the field was removed following adaptation, aftereffects were directed in the opposite direction to

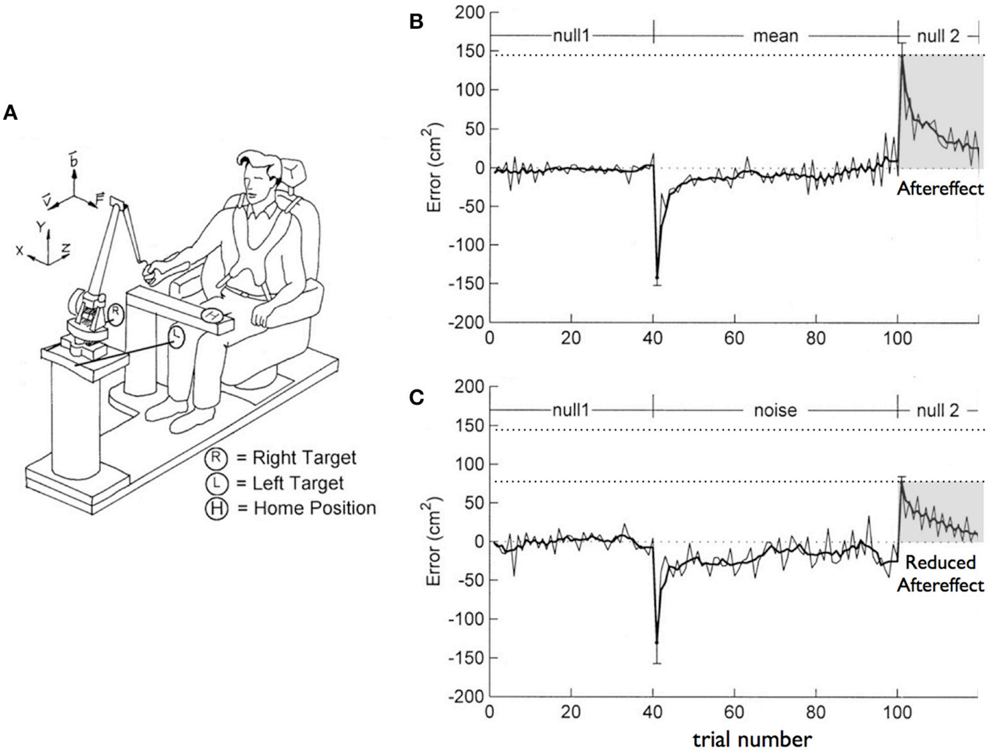


FIGURE 1 | (A) Experimental Setup. Subjects held a robotic manipulandum while reaching to targets to the left and right of midline. **(B)** Perpendicular errors during the course of the session in which subjects experienced the consistent field. **(C)** Perpendicular errors during the course of the session in which subjects experienced the inconsistent (noisy) field (from Takahashi et al., 2001).

the initial errors (**Figure 1B**, positive peak). Such aftereffects have previously been well-characterized, and are thought to represent predictive mechanisms that account for the previously applied field (Lackner and DiZio, 1998; Wang et al., 2001; Hwang and Shadmehr, 2005). In this study, when subjects were exposed to the inconsistent amplitude field, they also adapted (**Figure 1C**, positive peak). However, following adaptation, the amplitude of the aftereffects were substantially smaller than that following the consistent field. These results indicated the addition of impedance mechanisms that helped reduce the amplitude of errors. Trial-to-trial analysis revealed that impedance mechanisms were used in combination with predictive control to reduce the effects of unanticipated variations in force. This study, as well as a number of related adaptation studies (Ghez et al., 2007; Scheidt and Ghez, 2007; Yadav and Sainburg, 2014), demonstrated the use of a hybrid control strategy, exploiting both predictive and impedance mechanisms for efficient and robust coordination of arm movements.

LATERALIZATION OF PREDICTIVE CONTROL MECHANISMS

There has been substantial evidence that the two control mechanisms described above are specialized in different cerebral hemispheres, imparting different control characteristics to each arm. In a number of previous studies, we have characterized dominant arm advantages for predictive control during reaching movements (Sainburg and Kalakanis, 2000; Bagesteiro and Sainburg, 2002; Sainburg, 2002, 2005; Duff and Sainburg, 2007; Wang and Sainburg, 2007; Shabbott and Sainburg, 2008; Tomlinson and Sainburg, 2012; Mutha et al., 2013; Yadav and Sainburg, 2014). **Figure 2** shows the general experimental set up for our reaching studies. Subjects are seated in front of a table, while an air jet system allows the arms to glide over the surface, thus minimizing the effects of both friction and gravity. A virtual reality interface is projected on a mirror, placed horizontally above the arm, and under a 55″ HDTV monitor. This allows projection of a virtual or veridical location for a cursor, that represents the subjects' hand position.

Figure 3 shows examples of left and right arm horizontal plane reaching movements, performed rapidly without visual feedback, for a typical right-handed individual (Bagesteiro and Sainburg, 2002). As reflected by the graphs at the right, when dominant and non-dominant arm movements are matched for speed, dominant trajectories are substantially straighter, but tend to have slightly larger final position errors than non-dominant arm movements. In contrast, non-dominant trajectories tend to be deviated away from the target position, curving back toward the target at the end of motion. **Figure 3** (middle) shows the elbow joint kinetics associated with these two movements. Most notable is the fact that the computed muscle torque profile, reflecting muscle actions, remains near zero throughout the dominant arm movement. Nevertheless, the elbow achieves substantial net torque because the dominant controller efficiently exploits the interaction torque (dashed) that results from shoulder motion to drive the elbow joint into extension. In contrast, the non-dominant

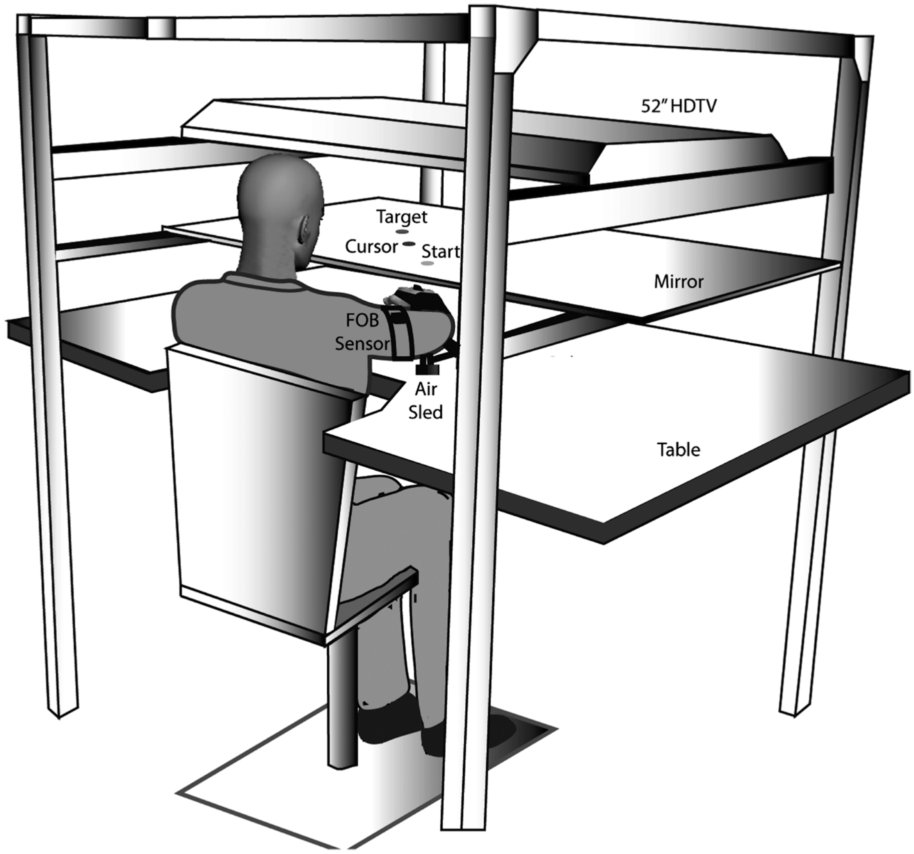


FIGURE 2 | Experimental set-up: Subjects sat facing a table with their arm supported in an air-sled over the horizontal surface by an air-jet system. An LCD screen was positioned above the mirror, which reflected a 2-D virtual reality environment, in which a start position and target were presented (from Yadav and Sainburg, 2014).

arm generates excessive elbow muscle torque that combines with interaction torque to deviate the hand path laterally. The result is the generation of a directionally inaccurate movement that requires substantially greater muscle torque at both joints to generate the same speed movement to the target. As reflected by the bar plots in **Figure 3** (bottom), dominant arm movements used substantially less integrated shoulder and elbow muscle torque to achieve comparable movement distances, speeds, and accuracies. This supports the idea that dominant arm movements are characterized by a control strategy that takes advantage of non-muscular forces. Nevertheless, non-dominant movements tend to achieve equal or slightly better final position accuracies, probably related to impedance control that can achieve accurate steady state positions. We have corroborated these findings in vertical reaching movements, performed without support (Tomlinson and Sainburg, 2012), and in left-handers (Przybyla et al., 2012). In related studies, we have confirmed that both energetic costs, and normalized muscle activities are higher in non-dominant arm reaching movements, while final position errors tend to be lower (Sainburg and Kalakanis, 2000; Bagesteiro and Sainburg, 2003).

Similar findings have been reported for different types of movements from other research groups. For example Pigeon et al. (2013) reported interlimb differences in coordinated turn-and-reach movements performed while standing. As shown in **Figure 4**, right handed subjects reached to 3 targets on the left of midline with the right arm, and 3 targets on the right of midline with the left arm. Movements were performed at two speeds (slow and fast) and under two loading conditions (1 lb weight, no weight). Due to the required trunk rotation, substantial Coriolis forces acted perpendicular to the target direction. As reflected by the paths in **Figure 4**, dominant arm movements were straighter and were minimally affected by the speed and weight conditions. In contrast, non-dominant arm movements were deviated laterally, more curved, and varied substantially with mass and speed conditions. Thus, the dominant arm was able to take account of the non-muscular Coriolis forces generated by trunk rotation, whereas non-dominant arm movements were substantially deviated by these interactions. Nevertheless, non-dominant arm movements curved back toward the targets at the end of motion, and were slightly more accurate with respect to radial errors at the final steady-state position.

Hore and colleagues extended these findings to overarm throwing movements. They conducted a series of studies of overarm throwing in the dominant and non-dominant arms, demonstrating that dominant arm movements take advantage of the whipping actions of interaction torques to generate accurate and high velocity motions of the hand at ball release (Hore et al., 1996, 1999, 2005; Debicki et al., 2004, 2011). In fact,

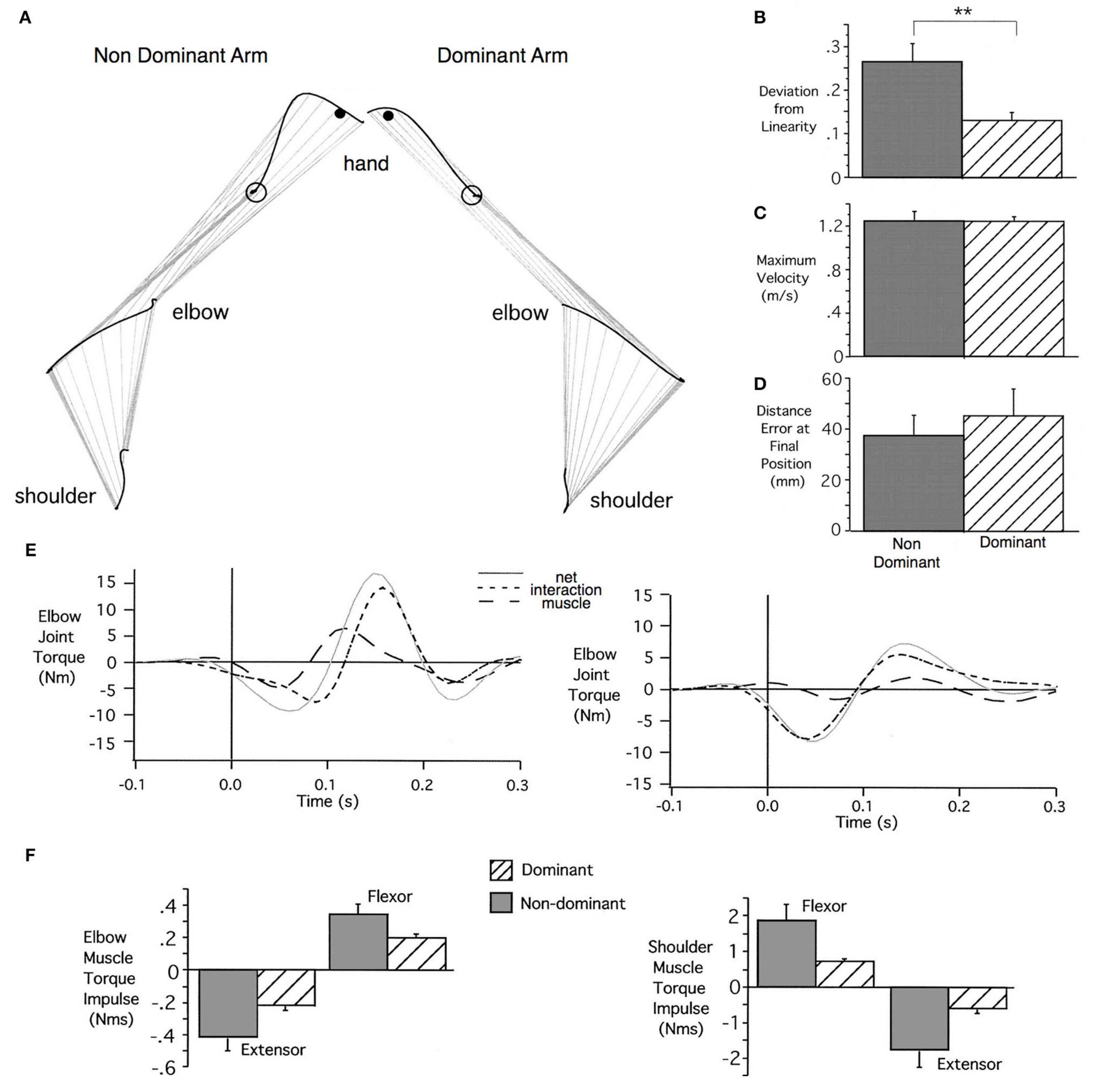


FIGURE 3 | (A) Shoulder, elbow, and hand trajectories from typical left (non-dominant) and right (dominant) hand arm movements toward a medial target. **(B–D)** Mean's ± *SE* for Deviation from Linearity **(B)**, Maximum Velocity **(C)**, and Distance Errors **(D)** for all movements across all subjects. **(E)** Elbow joint torque profiles include muscle torque, interaction torque, and net torque. **(F)** Group mean's ± *SE* for integrated flexor (positive) and extensor (negative) elbow and shoulder joint muscle torques (from Bagesteiro and Sainburg, 2002).

for the dominant arm, coordination patterns between the joints was qualitatively different for slow and fast throws, as subjects incorporated non-muscular interaction torques into the faster motions. In contrast, the non-dominant arm did not exploit these interactions, but instead exhibited the same intersegmental coordination patterns for both fast and slow movements. Thus, the greater-skill of the dominant arm was associated with the exploitation of non-muscular intersegmental interaction torques for rapid throwing motions. Heuer further extended this line of research to include tapping-like movements of the fingers (Heuer, 2007). During rapid finger oscillations, the dominant hand coordination strategy was shown to exploit non-muscular forces, while the non-dominant arm used excessive muscle co-contraction to impede the action of such forces. This resulted in greater efficiency and temporal consistency in motions of the dominant arm.

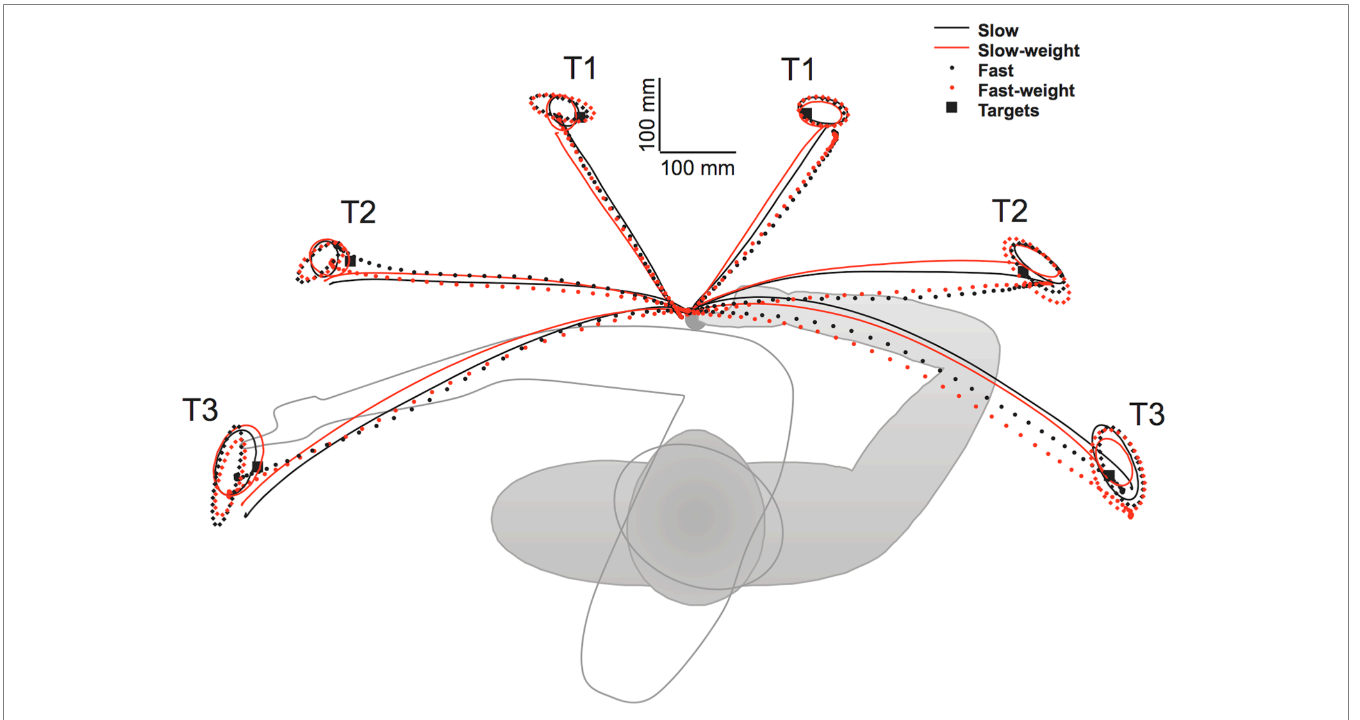


FIGURE 4 | Experimental set-up and averaged trajectories for turn and reach movements made with the left (right side of workspace) and right (left side of workspace) hands of right-handers under both speed (slow, fast) and weight (weight, no weight) conditions. Ellipses depict 95% confidence intervals for end point distributions under each condition (from Pigeon et al., 2013).

Taken together, these studies demonstrate that the dominant system is able to account for and exploit limb and task dynamics to make well-directed, smooth, and energetically efficient movements. Non-dominant movements tend to be less-efficient, and are often perturbed by non-muscular interactions. These findings lead to the conclusion that the left hemisphere (in right handers) control system is specialized for coordinating limb and task dynamics, a process that has been shown to rely on feedforward use of vision and proprioception in predictive control processes (Ghez et al., 1990, 1994, 1995; Sainburg et al., 1993; Gordon et al., 1994; Ghez and Sainburg, 1995).

LATERALIZATION OF IMPEDANCE CONTROL MECHANISMS

As elaborated above, even though the non-dominant arm tends to make less energetically efficient movements that are deviated by non-muscular forces, the final steady state position accuracy tends to be as good or better than that of the dominant arm. This likely reflects the exploitation of positional impedance mechanisms that can specify stiffness about equilibrium postures (Foisy and Feldman, 2006). In fact, a variety of studies have converged to suggest that the non-dominant arm exploits impedance mechanisms to generate accurate and stable arm movements. Studies of non-dominant arm adaptation to consistent viscous (Schabowsky et al., 2007) and inertial (Duff and Sainburg, 2007) loads have shown that adaptation occurs largely by impeding the trajectory deviations imposed by the force fields, rather than by specifically countering the fields through predictive mechanisms. While the non-dominant arm adapts to the applied force fields, aftereffects, reflecting predictive control mechanisms, tend to be small and inconsistent. In contrast, dominant arm adaptation to the same fields is characterized by large aftereffects that mirror the initial errors introduced by exposure to the forces. These findings support the hypothesis that impedance mechanisms are exploited to a greater extent by the non-dominant arm during adaptation to novel force fields. It has also been shown that the non-dominant arm responds to unexpected inertial loading with greater final position accuracy than the dominant arm (Bagesteiro and Sainburg, 2003). These findings suggest that the impedance control mechanisms employed for non-dominant arm control might be based, to some extent, on proprioceptive feedback loops. This may, in turn, be related to findings that the non-dominant arm shows an advantage in proprioceptive matching tasks (Goble et al., 2006, 2009; Goble and Brown, 2008a). In addition, the non-dominant arm tends to achieve more accurate final positions, when reaching movements are made without visual feedback of the hand, toward a large number of targets throughout the workspace (Oyama, 2012; Przybyla et al., 2013). Thus, the non-dominant arm exploits impedance control mechanisms to a greater extent than predictive mechanisms when adapting to novel dynamic conditions, and tends to achieve more accurate steady state positions, when confronted with unexpected inertial loads, or requirements for achieving steady state positions without the aid of visual feedback. Together, these findings provide support to the idea that the right hemisphere (in right handers) controller relies on impedance control mechanisms that exploit proprioceptive feedback loops to specify steady state limb configurations.

We designed an experiment to specifically address whether the non-dominant arm might optimize positional stability by specifying impedance around equilibrium positions, while dominant arm movements rely on predictive mechanisms that specify movement trajectories (Mutha et al., 2013). In a targeted-reaching experiment, we covertly and occasionally shifted the starting position of the hand, perpendicular to the direction of the target. We hypothesized that non-dominant control is specialized for achieving stable postures by specifying impedance around "equilibrium" positions. For goal-directed arm movements, this control mechanism should specify a "threshold" or "referent" configuration for the arm, similar to that proposed by the equilibrium point hypothesis (Feldman et al., 1995, 2011; Foisy and Feldman, 2006). Consistent with this, the non-dominant arm often shows better accuracy and precision in achieving a desired spatial position, particularly when an ongoing movement is perturbed (Bagesteiro and Sainburg, 2003; Duff and Sainburg, 2007; Przybyla et al., 2013). We, thus predicted that under conditions in which the starting position of the hand is shifted perpendicular to the target direction, non-dominant arm movements should reproduce the final equilibrium position of the baseline movements, whereas the dominant arm trajectory should parallel that of the baseline movements. The results of this study are represented in **Figure 5**. Dominant arm movements (Right) largely paralleled baseline movements and thus had smaller direction differences (direction errors-bar plot), than baseline movements. In contrast, non-dominant arm movements converged to the baseline final position and had larger direction differences than baseline movements. However, it is important to note that non-dominant arm movements did not completely converge onto the baseline target. The angular deviation was about 60% of that required to land the arm exactly on that target. Similarly, dominant arm movements were not completely parallel to baseline trajectories, especially for the medial displacements. These results suggest that each arm uses a predominant strategy, but not an exclusive control strategy. Thus, the dominant arm relies mostly on predictive control, but also employs impedance mechanisms, and vice versa for the non-dominant arm. This evidence provides support for hybrid control of each arm.

COMPUTATIONAL HYBRID-CONTROL SIMULATION

The evidence provided above suggests that hybrid control might be the foundation for handedness. In order to examine the plausibility of our hypothesized hybrid control scheme, we developed a computational simulation that combined predictive control of limb dynamics with impedance control mechanisms, in a serial control scheme, to characterize the differences between the trajectories of dominant and non-dominant arm movements. In this simulation, the movements of both the arms were initiated using predictive control mechanisms, and terminated using impedance mechanisms (Yadav and Sainburg, 2011, 2014, Neuroscience). We reasoned that the different coordination patterns between the limbs might reflect the degree to which the movement depends on each mechanism during its course, which we characterized in this simulation as the time that control switched from predictive to impedance mechanisms. Four parameters were used to

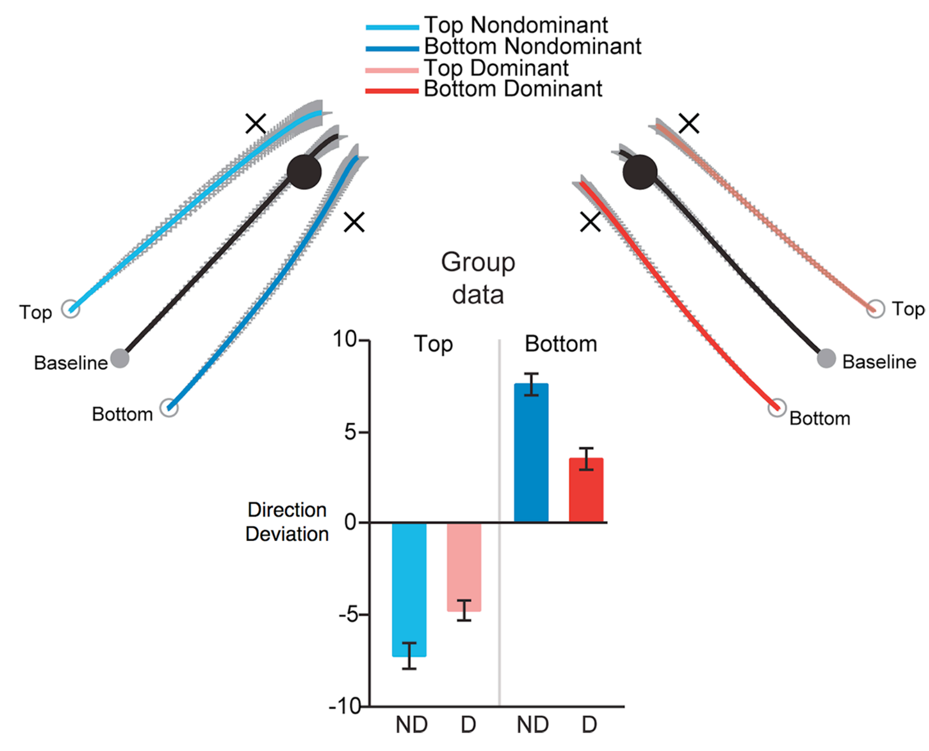


FIGURE 5 | Groups means for trajectories (normalized and averaged across subjects) made toward targets under baseline (black) and from displaced initial positions, for dominant (red) and non-dominant (blue) arms. Bar plots (right) show mean ± *SE* for direction error, measured as the difference in the direction of displaced and baseline movements, measured at final position (from Mutha et al., 2013).

characterize predictive control, four parameters for impedance control, and a 9th parameter described the instant of switch between the two modes of control. We predicted an early switch to impedance control for the non-dominant arm, but a late switch, near the end of motion, for the dominant arm. **Figure 6** shows the results of this simulation for different switch times during the course of a typical movement. Note that these trajectories are shown in a right hand coordinate system. For early switches to impedance control (left side of **Figure 6**), movements were deviated laterally, and curved back toward the target at the end of motion, while late switches (right side of **Figure 6**) are fairly straight. These different trajectories are very similar to the right and left arm paths shown in **Figure 3** for rapid, horizontal plane reaching movements. In fact, when we optimally fit our model to subjects' movements, the more curved trajectories of the non-dominant arm were best characterized by a significantly earlier switch to impedance mechanisms than when the model was fit to dominant arm movements. The trajectories of the dominant arm were best fit, when the switch to impedance mechanisms occurred late in the deceleration phase of motion. This simulation provided confirmation that hybrid control using both impedance and predictive control mechanisms is plausible and might explain the trajectory differences of dominant and non-dominant arm reaching movements.

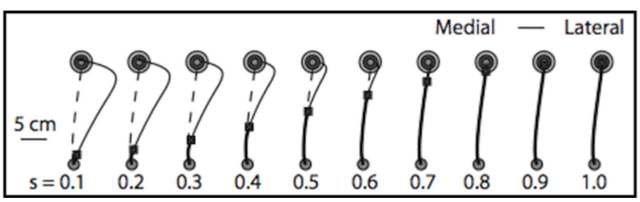
THE EFFECTS OF HYBRID CONTROL ON MOTOR PERFORMANCE AND ADAPTATION

In a direct test of the hypothesis that the non-dominant arm exploits predominantly impedance mechanisms, while the dominant arm exploits predominantly predictive mechanisms for control, we designed a study (Yadav and Sainburg, 2014) that employed a similar paradigm to that introduced by Takahashi et al. (2001). However, rather than exposing only the dominant arm to a predictable and unpredictable field, we exposed each arm to the both fields. Each force field was imposed by a robotic manipulandum attached to the arm support. The field that was designed to advantage the predictive controller had a consistent magnitude between trials, that varied with the square of hand velocity. The field designed to advantage the impedance controller had an inconsistent magnitude between trials that varied linearly with hand velocity. Because the velocity-square field did not change the form of the equations of motion for the reaching arm, we reasoned that a forward dynamic-type controller should perform well in this field, while control of linear damping and stiffness terms should be less effective. In contrast, the unpredictable linear field should be most compatible with impedance control, but incompatible with predictive dynamics control. Our hypothesis predicted an arm X field interaction, such that the dominant arm should perform best within the consistent field, and the non-dominant arm in the inconsistent field. **Figure 7** shows the results of this experiment, quantified by mean squared jerk, a measure that varies inversely with movement smoothness (Left), and movement duration (right). Both measures of performance showed a hand X field interaction, such that dominant arm movements were performed smoother and faster within the predictable field, while non-dominant arm movements were performed smoother and faster within the unpredictable field. These findings corroborated our hypothesis that motor lateralization might reflect asymmetries in specific motor control mechanisms associated with predictive control of limb and task dynamics, and control of limb impedance.

IS HYBRID CONTROL OF LIMB DYNAMICS AND LIMB IMPEDANCE BASED ON HEMISPHERIC SPECIALIZATIONS?

Previous studies have demonstrated that following unilateral stroke, motor impairment occurs both contralateral, as well as ipsilateral to the lesion (Wyke, 1967; Winstein and Pohl, 1995; Hermsdorfer et al., 1999b; Swinnen et al., 2002; Haaland et al., 2004, 2009; Yarosh et al., 2004; Wetter et al., 2005; Sainburg and Duff, 2006; Schaefer et al., 2007, 2009a; Chestnut and Haaland, 2008). Although ipsilesional impairments can be functionally limiting, they can also provide important insight into the role of the ipsilateral hemisphere in controlling movement. Specifically, the lateralization of specific motor control mechanisms can be examined, given that unilateral arm movements are thought to recruit processes in both hemispheres. Our hypothesis of hybrid control has two important predictions for unilateral brain lesions that affect sensorimotor function: First, because we hypothesize that both hemispheres contribute different mechanisms to each arm, unilateral hemisphere lesions should produce hemisphere specific deficits in the ipsilesional arm of stroke patients. Therefore, control of the ipsilesional arm should reflect a greater influence from contributions of the contralesional controller, when compared with the same arm of age matched control subjects. We limited our analysis to patients with right handedness, given the lack of normative data on lefties, and because of restrictions in recruitment. We initially focused our study on patients with significant hemiparesis, on the contralesional side of the body.

Non-dominant arm like
(curved lateral to medial)



Dominant arm like
(curved medial to lateral)

FIGURE 6 | Simulated trajectories for different switch times between predictive and impedance controller. Dashed line shows pure optimal predictive controller. Early switch times **(Left)** are controlled almost entirely by the impedance control algorithm, while late switch times **(Right)** are almost entirely controlled through optimal predictive control (form Yadav and Sainburg, 2014).

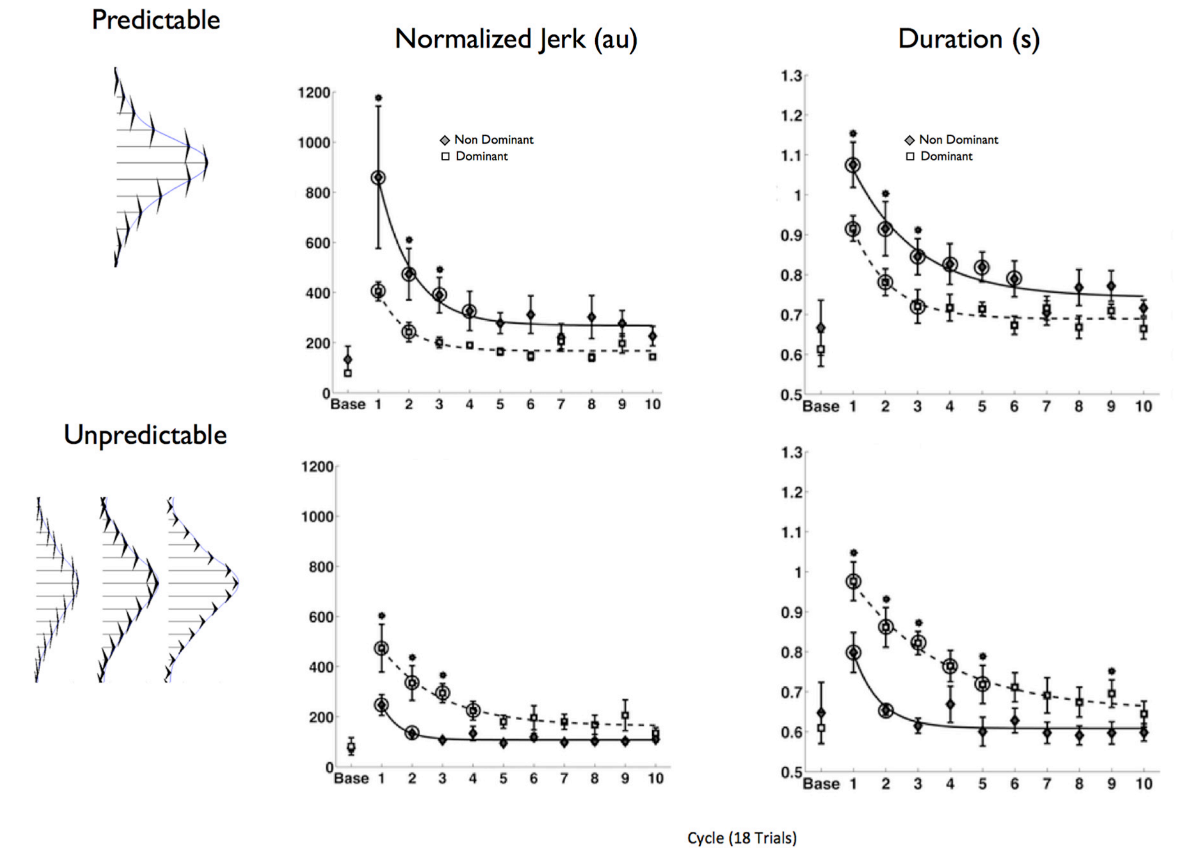


FIGURE 7 | Force field structure is shown at right: fields were generated perpendicular to the direction of the target, and varied with either the square of velocity (predictable field) or linearly with velocity (unpredictable). Group mean ± *SE* for mean squared jerk **(Left)** and movement duration **(Right)** are shown across all 180 movements (18 cycles). Baseline performance is shown at the left of each plot (form Yadav and Sainburg, 2014).

The main purpose of this study was to examine whether our dynamic dominance model of motor lateralization could predict hemisphere specific motor deficits in stroke patients (Schaefer et al., 2009a). Chronic stroke patients with either left or right hemisphere damage (LHD or RHD) used their ipsilesional arm, and the control subjects used either their left or right arm (LHC or RHC), to perform targeted reaching movements in different directions within the workspace ipsilateral to their reaching arm. We used structural MRI images to quantify the location and volume of each subjects' lesion, in order to match lesion characteristics between our LHD and RHD groups (see **Figure 8**). The results of the study are depicted in **Figure 9**, which shows variability in performance at two points in the movement, at peak velocity, or at the final position. The ellipses reflect 95% confidence intervals around the cloud of hand path points for representative patients with left and right hemisphere damaged patients. LHD patients had greater variabilities early in movement and significantly greater initial direction errors and trajectory curvatures than both age matched control subjects (LHC) and RHD patients. In contrast, RHD patients showed lower initial trajectory variabilities and trajectory deviations, but greater final position variances and errors than both their control group and LHD patients. Left hemsiphere damage produced deficits in controlling the ipsilesional arm trajectory, whereas the RHD group showed deficits in ipsilesional final position accuracy. These results extended our findings in asymmetrical control of each limb in healthy subjects to the cerebral hemispheres: We showed that each hemisphere contributes different control mechanisms to the ipsilesional arm. While the existence of spasticity and paresis precluded the examination of contralesional arm function in this group of patients, we later extended these findings to the contralesional arm in patients with very mild paresis (Mani et al., 2013). In addition, studies examining the role of each hemisphere in visuomotor adaptation paradigms have also supported the hypothesis that each hemisphere contributes different control processes to each arm: We found that LHD interfered with adaptation of initial direction, but not with the ability to adapt the final position of the ipsilesional arm. In contrast, RHD interfered with online corrections to the final position during the course of adaptation. These findings support our hypothesis that the control of trajectory and steady-state position may be lateralized to the left and right hemispheres, respectively (Schaefer et al., 2009b). Thus, substantial evidence in stroke patients supports the proposition that each hemisphere contributes hemisphere specific mechanisms to control of each arm.

FIGURE 8 | Lesion locations were traced on 11 axial slices (see insert for slice level) from MRI or CT scans for each LHD (1–7) and RHD (1–7) patient. Slices are displayed left-to-right from inferior to superior (i–xi) for both groups of patients. Arrows in top row indicate location of central sulcus (from Schaefer et al., 2009a).

IS ARM SELECTION RELATED TO MOTOR CONTROL ASYMMETRIES?

Handedness is most often measured by questionnaires that assess an individual's preference for using a particular hand to perform a variety of tasks. While such assessments have proved reliable, they do not address the underlying neurobehavioral processes that give rise to the choice of which hand to use. The result is that preference measures can give quite different results under different task conditions (Stoloff et al., 2011; Habagishi et al., 2014). In fact, Coelho and colleagues have shown that choice of hand is subordinated to other task constraints, such as the maneuverability of the hand, following retrieval of an object, when the two are set up in a competing paradigm (Coelho et al., 2014). Thus, it is clear that arm selection is not simply a reflection of lateralization of motor performance, but results from an interaction between control asymmetries and task requirements.

In order to better understand this interaction, we recently conducted a series of studies based on the hypothesis that an individual's choice of which hand to use for a given task should result from an interaction between the underlying control asymmetries with task conditions (Przybyla et al., 2013; Mani et al., 2014). We tested this hypothesis by manipulating two factors in targeted reaching movements that differentially affect limb performance: Region of workspace, and visual feedback condition. The first manipulation modified the geometric and dynamic requirements of the task for each arm across 32 targets that occupied a large range of the reachable horizontal workspace in front of the subject. The second variable, visual feedback condition, modified the sensorimotor performance asymmetries. Previous evidence indicated that the non-dominant left arm often shows equal or greater accuracy compared to the dominant right arm, when performing reaching movements in the absence of visual feedback, but worse accuracy when vision is available (Guiard et al., 1983; Carson et al., 1990; Imanaka et al., 1995; Lenhard and Hoffmann, 2007; Goble and Brown, 2008b). This is likely related to the fact that dominant arm predictive processes are dependent upon vision for updating, and degrade in the absence of visual information (Ghez et al., 1994). However, non-dominant arm control appears

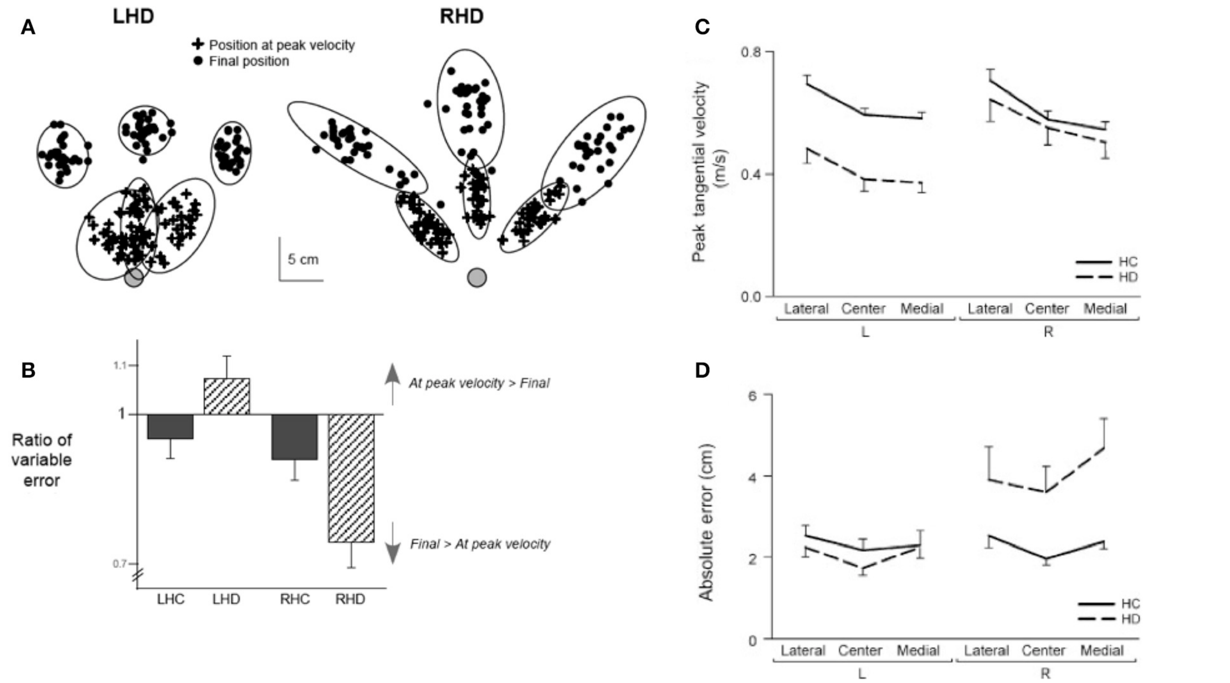


FIGURE 9 | (A) Sample positional variation plots, with 95% confidence intervals, shown by ellipse, for an example LHD patient and RHD patient. **(B)** Group data shows ratio of positional variation at peak velocity divided by positional variation at the end of movement for LHD, RHD, left hemisphere control group (LHC), and right hemisphere control group (RHC). **(C)** Mean ± *SE* for peak velocity and **(D)** absolute final position error for all four groups (LHD, RHD, LHC, RHC) for movements to each target (from Schaefer et al., 2009a).

to be less dependent upon visual information, which is consistent with the idea that non-dominant control relies more completely on proprioceptive information (Bagesteiro and Sainburg, 2002; Goble and Brown, 2010). Thus, we reasoned that manipulating visual feedback allowed us to experimentally vary the relative performance advantages between the arms, providing an advantage of the non-dominant arm under no-vision conditions, and to the dominant arm under vision conditions.

Our results confirmed these predictions, demonstrating a substantial advantage for the non-dominant arm when performing in the absence of visual feedback, and for the dominant arm with visual feedback. In addition, removing visual feedback increased the choice to use the non-dominant arm to reach toward targets near midline, an effect that was enhanced for targets requiring larger movement amplitudes. These results showed that limb choice is an interactive process, based on current sensorimotor conditions, in the context of a given task. Most importantly, these results support the view that limb selection emerges from the underlying control processes that confer advantages to each limb under specific task conditions. While these underlying neural processes appear to be constant, they can result in either limb experiencing performance advantages, depending on task conditions. Thus, limb selection should be viewed as an emergent phenomenon that results from the interaction between lateralization of basic motor control processes with current task conditions. For this reason, limb selection should not be viewed as a primary factor in either measuring or in defining motor lateralization.

SUMMARY AND CONCLUSIONS

This paper presented evidence for the Dynamic Dominance Model of motor lateralization that proposes a left hemisphere (in right-handers) specialization for processes that predict the effects of limb and task dynamics, given consistent mechanical conditions, and a right hemisphere specialization for impedance control mechanisms that can minimize potential errors when faced with unexpected mechanical events. This model forms a motor specific component to the broader paradigm of brain lateralization that has been proposed by Rogers et al. (MacNeilage et al., 2009). Roger's model attributes specialization of the left-hemisphere of the vertebrate brain to well-established patterns of behavior performed in familiar environmental conditions, while the right hemisphere is seen as specialized for responding to unforeseen environmental events. The dynamic dominance model of motor lateralization seems to form the motor specific analog to these specializations. The fit between these two models is particularly impressive, given that the research was derived independently. Roger's model was developed by seeking fundamental principles that could explain a wide variety of experimental and natural observations of behavior across a range of vertebrate species. The dynamic dominance hypothesis was independently developed by seeking an organizational principle that could account for motor asymmetries in humans, and hemisphere specific motor deficits in patients with unilateral brain lesions. Both hypotheses seem to converge in supporting a global framework for understanding the biology of motor lateralization.

Rogers model presents an elegant organizing principle that can encompass a large array of emotional, language, perceptual, and cognitive asymmetries across a spectrum of vertebrate species. However, it remained unclear how exactly handedness might fit into this model. Certainly, it is well-established that humans and certain species of non-human primates (Hopkins and Bard, 1993; Hopkins and Bennett, 1994; Hopkins and Cantalupo, 2004; Hopkins and Russell, 2004; Hopkins et al., 2005) prefer the right hand for performance of tasks using tools, for overhand throwing, and other skilled behaviors. Further, these tasks could be considered as best performed in predictable environmental circumstances. However, the fit between these observations of arm preference and the model expressed by Rogers has not been clear, nor has the role of the non-dominant arm within this scheme been elaborated. Over the past few decades, studies of motor coordination in healthy individuals and of hemisphere specific deficits in stroke patients have provided evidence for an explanation of handedness that is based on fundamental motor control principles. The role that each mechanism contributes to control depends on the predictability and consistency of the mechanical environment. Impedance control processes take precedence under unpredictable and unstable mechanical environments, while predictive processes prevail when environmental conditions are consistent and predictable. Right hemisphere processes that impart impedance control to the limbs lead to robust, but inefficient behavior, whereas left hemisphere processes that provide for predictive control can lead to energetically efficient coordination patterns. This paper has reviewed substantial evidence that these two aspects of control are specialized in different cerebral hemispheres, imparting different control characteristics to each arm. This has been shown across a range of movements, including horizontal and vertical reaching movements, turn and reach movements, overhand throwing, and through studies of adaptation to novel force environments and to novel visuomotor distortions.

In conclusion, handedness results from the hybridization of predictive and impedance control mechanisms, which have become specialized to different hemispheres. The integration of both control mechanisms into unimanual limb movements ensures both optimality of movement and robustness against unpredictable mechanical conditions. Rogers and colleagues have provided evidence that hemispheric specialization allows for efficient performance of potentially competing neural processes, which emphasizes the importance of lateralization in optimal and adaptive behavior. This view of lateralization provides a fundamental explanation of the motor control mechanisms that result in the emergence of motor performance asymmetries.

While the majority of the studies cited in this paper addressed right-handed individuals, similar findings have also been shown for left handers (Przybyla et al., 2012), suggesting that both expressions of handedness might reflect the same but mirror imaged organization. However, it should be stressed that left-handers often show more symmetric motor behavior, and the extent rather than the direction, of handedness might represent very different neural phenomenon. Because lateralization appears to reflect an optimization process, lack of such lateralization should result in poor integration of predictive with impedance processes for movement control. This should lead to less effective prediction of limb dynamics and lower ability to stabilize against unpredicted perturbations. Such incoordination might be related to fact that children with developmental coordination disorder tend to show lower laterality indices (Hill and Bishop, 1998). However, it is also possible in some individuals that symmetry in behavior could be associated with greater function, as well as greater neural lateralization. In fact, it has been shown that when individuals suffer an amputation of their dominant right arm, they learn to use the previously non-dominant arm as their dominant controller. After years of practice, the non-dominant left arm functions comparably with age matched subjects' dominant arms. This improvement in function of the non-dominant arm is associated with greater activation of ipsilateral cortex, indicating that practice using the non-dominant arm did not cause the nervous system to become symmetric, but rather led to greater access of the lateralized neural system during movement control (Philip and Frey, 2014). This suggests a plasticity in the control system that could allow greater symmetry of function through practice. Thus, it is likely that symmetry in motor performance and preference may represent either optimization of a lateralized neural system, or lack of neural lateralization, which would likely lead to deficiencies in coordination. While this proposition is highly speculative, it provides predictions that can be directly tested through empirical research methods.

FUNDING

This work was supported by #R01 HD059783 from the National Institutes of Health (NIH): NICHD. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 19 August 2014; accepted: 09 September 2014; published online: 08 October 2014.

Citation: Sainburg RL (2014) Convergent models of handedness and brain lateralization. Front. Psychol. ***5****:1092. doi: 10.3389/fpsyg.2014.01092*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

OPINION ARTICLE
published: 11 November 2014
doi: 10.3389/fpsyg.2014.01300

Handedness genetics: considering the phenotype

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Keywords: handedness, genotype, phenotype, laterality, hemispheric asymmetry, hemispheric lateralization, motor control, ontogenesis

The question which genetic, epigenetic and environmental factors contribute to human handedness certainly is one of the central questions in research on manual asymmetries. A number of environmental factors such as season of birth (Stoyanov et al., 2011), cultural influences (Fagard and Dahmen, 2004), differential visual experience of the hands (Ocklenburg and Güntürkün, 2009; Ocklenburg et al., 2010), parental influence (Laland, 2008) and others (Schaafsma et al., 2009) have been shown to influence handedness. Moreover, several genes such as *LRRTM1* (Francks et al., 2007), *PCSK6* (Scerri et al., 2011; Arning et al., 2013), and *AR* (Medland et al., 2005; Hampson and Sankar, 2012) have been related to handedness. However, the variance in individual handedness explained by any single one of these factors is typically low, and it is not uncommon that findings in one sample cannot be replicated in others (for example see: Bloss et al., 2010; Hubacek et al., 2013). Furthermore, hardly anything is known about epigenetic and epistatic interactions between different genetic and environmental factors influencing handedness. In view of this, several authors recently argued that only a complex multifactorial model could explain the ontogenesis of handedness (e.g., McManus et al., 2013; Ocklenburg et al., 2013; Armour et al., 2014). McManus et al. (2013) estimated the number of genetic loci involved in handedness to be at least 30–40, and possibly much larger. This estimation suggests that genome-wide association studies with very large sample sizes might constitute a meaningful methodological tool to further advance our knowledge about how handedness develops. In our opinion, however, the large number of involved ontogenetic factors and likely complex interactions between them is only part of the problem why the search for the biological determinants involved in the development of handedness despite continuous research still is at a very early stage.

While a definition of handedness seems trivial at first glance, the term "handedness" actually has been used to describe a number of surprisingly different concepts, rendering clarification necessary. First, as discussed in a recent review article by Scharoun and Bryden (2014), there is an important distinction between *hand preference* and *hand performance*. *Hand preference* commonly is assessed with questionnaires such as the widely used Edinburgh Handedness Inventory (EHI, Oldfield, 1971). The EHI identifies an individual's subjectively preferred hand for 10 different manual activities (e.g., writing or striking a match). A lateralization quotient (LQ) is calculated using the formula $LQ = [(R - L)/(R + L)]*100$, with R indicating the number of activities for which the right hand is preferentially used, and L indicating the number of activities for which the left hand is preferentially used. The LQ ranges between -100 and $+100$, with negative values indicating a larger number of left-hand preferences, and positive values indicating a larger number of right-hand preferences. While some authors developed behavioral approaches to assess hand preference (e.g., Calvert and Bishop, 1998), the overwhelming majority of researchers uses questionnaires such as the EHI to assess hand preference.

Hand performance, on the other hand, typically is assessed with motor tasks such as the widely used peg board task (e.g., Annett, 1985, 2002; Scerri et al., 2011). In this task, the time participants need to move a row of 10 pegs from one side of a board to the other is measured. A quantitative value of asymmetry in hand performance is obtained by comparing reaction times for left and right hand. Other hand performance tasks include placing dots in circles or squares on a sheet of paper as quickly as possible (McManus, 1985; Tapley and Bryden, 1985), or picking up 20 matches placed on a table as quickly as possible (McManus, 1985). Interestingly, tests of hand preference and hand performance yield significantly different distributions (Peters and Durding, 1978; Nicholls et al., 2010). Hand preference typically has a J-shaped (and hence bimodal) distribution with a large number of strongly right-handed individuals, a smaller number of strongly left-handed individuals, and few individuals in between, e.g., ambidextrous to some degree, and some authors have argued that handedness in fact is a dichotomous variable (e.g., McManus, 2002; also see Corballis et al., 2012 for an overview).

In contrast, hand performance measured with the peg board task typically shows a more unimodal distribution with a shift to the right side (Annett, 1985). However, McManus (1985) has argued that the peg board data are also bimodal, and that the assumed unimodality might be an artifact of measurement noise, since a high amount of noise in the data could make it possible that a smaller distribution of left-handers is hidden in the tail of the larger distribution of the right-handers. While the details of this discussion go beyond the scope of this Opinion article, it is also important to mention that the distribution of hand performance data seems to be task-dependent to a large extent, with some tasks (e.g., McManus, 1985; Tapley and Bryden, 1985) clearly showing more bimodal distributions than the peg board task.

Although hand performance and hand preference seem to be related, the correlation between them strongly depends on the tasks used to assess the two parameters. For example, while Badzakova-Trajkov et al. (2011) found a strong correlation between hand preference and hand performance scores ($r = 0.72$), a recent study by Geuze et al. (2012), reported much lower correlation coefficients. In this study, the correlation between hand preference and peg board performance was 0.09, while it was 0.03 for hand preference and grip force, and 0.19 for hand preference and ball throwing accuracy. Moreover, even though the correlations with peg board task performance and ball throwing accuracy reached significance, none of the correlation coefficients indicated a particularly strong association. While the striking difference between the two studies may be partly due to differential percentages of left- and right-handers in the two samples (in the Badzakova-Trajkov et al., 2011, sample there were 23 left-handed, 48 mixed-handed and 64 right-handed participants while in the Geuze et al., 2012, sample there were 15 left-handed, 8 mixed-handed and 598 right-handed participants) there is clearly more research on the complex relation of hand preference and hand performance needed. Interestingly, it has also been shown that hand preference correlates with certain cognitive variables, like magical ideation and creative achievement, while hand performance does not (Badzakova-Trajkov et al., 2011). Taken together, these findings suggest that what is considered as handedness by different studies is not a uniform trait but might represent several different, distinct phenotypes.

This idea is also supported by the distinction of handedness direction and handedness consistency. Handedness direction is usually defined as the side of the preferred hand for fine motor activities, e.g., left-handed or right-handed, although some authors also use "mixed-handed" as a third category. This practice, however, has been strongly criticized by McManus (1996) who argued that mixed-handedness does not represent a natural category but rather a mixture of weak left-handers and weak right-handers. Instead, McManus (1996) suggests using a subdivision into four handedness groups (weak right, strong right, weak left, strong left) when further differentiation of handedness direction is desired. In contrast to direction, handedness consistency (some authors also use the term "handedness degree," e.g., by Prichard et al., 2013) is the specificity of the preference for using one hand over the other, e.g., if one hand is used for all task as opposed to one hand being used for some tasks and the other hand for others. Both handedness direction and handedness consistency can be calculated based on results of a handedness preference questionnaire or a handedness performance task.

Interestingly, Arning et al. (2013) demonstrated that a sequence variation (rs10523972) in *PCSK6* was significantly associated with handedness consistency but not with handedness direction. Individuals heterozygous for a long and a short allele of an intronic 33 bp variable-number tandem repeat polymorphism were more prone to inconsistent hand preference (e.g., performing most—but not all—tasks with one hand) than individuals homozygous for a long allele. In contrast, no association between this polymorphism and handedness direction was observed. It is therefore likely that handedness direction and consistency (or strength) represent distinct phenotypes. This idea is also supported by several studies showing that handedness consistency, but not handedness direction, is a systematic predictor of performance in several cognitive domains, e.g. episodic memory retrieval, cognitive flexibility and risk perception (see Prichard et al., 2013 for a comprehensive review article).

Interestingly, the view that direction and strength of hemispheric asymmetries represent two distinct, largely independent phenotypes is also supported by recent studies in zebrafish. In this species, behavioral lateralization is modulated by structural asymmetries in the epithalamus (Barth et al., 2005; Bianco and Wilson, 2009). Genetically, the occurrence of these epithalamic asymmetries is regulated by several genes within the *NODAL* pathway which generally is relevant for the determination of left-right asymmetry in embryonic development. When expression of this pathway is symmetrical or absent, structural asymmetry *per se* is still established but its direction is not leftward like in most wildtype fish, but completely random (Concha et al., 2000). Thus, strength and direction of these hemispheric asymmetries in zebrafish likely are controlled for by two different genetic pathways. This finding is particularly interesting since Brandler and Paracchini (2014) recently suggested the *NODAL* pathway to also be involved in the ontogenesis of human handedness.

Taken together, in our opinion the large number of possibly interacting genes and non-genetic factors is only one reason why it is so difficult to determine the ontogenetic bases of handedness and other forms of hemispheric asymmetries. Another reason is that we simply do not know enough about what exactly constitutes a handedness phenotype, and how many there are. For the time being, we would like to suggest that future studies on the genetics of hemispheric asymmetries should include both a preference measure (e.g., EHI) and a performance measure (e.g., the peg board task), and that both direction and strength should be reported for those two measures in addition to a composite score such as a laterality quotient. Furthermore, research on the genetics of handedness may benefit from a stronger integration of brain activation measures, e.g., motor cortex activation differences between left- and right-handers during finger tapping or similar tasks.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 05 September 2014; accepted: 26 October 2014; published online: 11 November 2014.

Citation: Ocklenburg S, Beste C and Arning L (2014) Handedness genetics: considering the phenotype. Front. Psychol. ***5****:1300. doi: 10.3389/fpsyg.2014.01300*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

MINI REVIEW ARTICLE
published: 13 January 2015
doi: 10.3389/fpsyg.2014.01587

Attentional asymmetries – cause or consequence of human right handedness?

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It is well established that the vast majority of the population favors their right hand when performing complex manual tasks. However, the developmental and evolutionary underpinnings of human manual asymmetries remain contentious. One often overlooked suggestion is that right handedness may stem from an asymmetrical bias in attention, with the right hand being allocated more attentional resources during bimanual tasks than the left hand (Peters, 1981). This review examines the evidence for attentional asymmetries during a variety of bimanual tasks, and critically evaluates the explanatory power of this hypothesis for explaining the depth and breadth of individual- and population-level manual asymmetries. We conclude that, while the attentional bias hypothesis is well-supported in adults, it requires further validation from a developmental perspective to explain the full breadth of adult manual laterality.

Keywords: handedness, laterality development, bimanual coordination, attention, motor control, laterality of motor control

Approximately 90% of humans consider themselves to be right handed (Coren and Porac, 1977). This unique manual asymmetry can be taken to have at least two related, but not entirely overlapping, meanings: (1) a higher level of skill when using the right hand for complex manual tasks and (2) a preference to select the right hand to perform most daily activities. Competing explanations for the cause and consequences of human handedness have tended to emphasize the asymmetries of performance or selection, implying that one drives the other. Other explanations have suggested that handedness is a consequence of the leftward lateralization of language present in the majority of the population (Annett, 2000).

The goal of this article is to provide an overview of the evidence for a rarely discussed hypothesis – that right handedness is a consequence of a rightward attentional bias. Proponents of this hypothesis claim that when attention must be divided between the hands during bimanual tasks, most individuals will allocate the majority of their attentional resources to the right hand or its task. First, we describe the evidence for an automatic link between the attentional system and manual actions. Next, we present the empirical studies which have found evidence for a rightward attentional bias in right-handed individuals' during rhythmic and discrete bimanual tasks. Finally, we discuss the viability of the attentional bias explanation as a way to bridge the gap between performance and selection asymmetries.

ATTENTIONAL YOKING WITH HAND MOVEMENTS

On the face of it, there would seem to be obvious advantages to having two equally skilled hands to complete twice as many tasks. Such a strategy, however, would not be easily compatible with humans' attentional limitations: prior to commencing a typical reach toward a visual target, a saccade is used to aim the high-resolution foveal portion of the eye to the region of interest (Desmurget et al., 1998; Flanagan and Johansson, 2003). Although this serial chain of events may seem obvious in a visually guided task, some evidence suggests that there is an automatic link between overt attention and action (for a recent critical review, see Smith and Schenk, 2012). Fisk and Goodale (1985) demonstrated that that saccades and hand movements toward visual targets are yoked together, with an eye movement's onset driven by the latency of the hand movement's onset. Similar conclusions have been drawn by Neggers and Bekkering (2000), whose experiment appeared to demonstrate that a new saccade cannot be planned until the preceding reach to a visually defined target has been completed. Furthermore, there is good evidence for a yoking between temporal aspects of hand and eye kinematics, with the time at which a saccade lands being well correlated with the time at which the reaching arm is at the point of peak acceleration (Helsen et al., 1998). Clinical evidence for a yoking between the eyes and hands comes from cases of 'magnetic misreaching' (Carey et al., 1997; Jackson et al., 2005), where patients with bilateral parietal lobe damage are unable to reach to any direction other than the target of their gaze (see also van Donkelaar and Adams, 2005). By contrast, Buxbaum and Coslett (1998) report an ataxic patient showing the opposite clinical sign, with the patient's gaze becoming spontaneously fixed upon his hand during movements, interfering with goal-directed activities.

The link between attention and action in the context of physiology and neuropsychology is well-studied in the context of sequential unimanual movements (for review, see Baldauf and Deubel, 2010). There is, however, far less research examining how the attentional systems behave when both hands are moving simultaneously or being coordinated to complete a task.

ATTENTIONAL ASYMMETRIES DURING RHYTHMIC BIMANUAL TASKS

The seminal study on attentional biases during bimanual coordination was undertaken by Peters (1981), who had participants tap one hand to the beat of a metronome (the easier task, with no inherent asymmetries) while the other hand tapped at its maximum rate (a more difficult task, where the dominant hand tends to excel) in a sample of left and right handers. Right-handed subjects experienced no difficulties when their right hand was performing the difficult rapid tapping task and their left hand was performing the easy metronomic tapping task. When tapping in the converse arrangement, however, the right handers suffered large performance decrements in both tasks. The critical link to attention can be inferred from the fact that it is not just the non-dominant hand which suffers, but rather that when the configuration is 'wrong,' both hands are equally impaired in their performance of their respective tasks. In other words, the poor performance seen in both the easy and difficult tasks when the left hand was assigned the more difficult job was a consequence of a rightward bias in attention rather than a motoric asymmetry.

This early demonstration of an attentional asymmetry has been followed by work examining subtle differences in between-hand coordination when participants are asked to move their hands back and forth synchronously at various frequencies. Treffner and Turvey (1995) examined right handers' ability to move a large pendulum held in each hand forward and backward in simple coordinative patterns. The authors found a tendency for the right hand to slightly lead the left hand when participants were instructed to move their hands synchronously. The attentional nature of this asymmetry was clarified in later work by Amazeen et al. (1997), who showed that the right hand lead was reduced when attention was directed away from the right hand and the overall variability (i.e., SD of relative phase) of the rhythmic movements was increased when attention was directed away from the dominant hand. In other words, when right-handed subjects perform an inherently low variability task they instead tend to perform with a slight right hand lead which appears to reflect their prior bias in attention, which can then be manipulated by altering the direction of overt attention, at the expense of overall performance variability. Interestingly, attending toward the right hand during similar bimanual tasks has been shown to increase this phase lead and improve performance in terms of variance as compared to free viewing or attending toward the left hand (Swinnen et al., 1996; Rogers et al., 1998). Thus, the performance in these tasks can be modulated by shifting attention, with individuals performing best when attending their right hand and performing worst when attending to their left hand (see also Treffner and Turvey, 1996).

ATTENTIONAL ASYMMETRIES DURING DISCRETE BIMANUAL TASKS

The most straightforward method of investigating attention during discrete bimanual movement has been to examine eye movements during bimanual reaches toward visual targets. Early work examining the horizontal direction of right-handed participant's eye movements using electrooculography during rapid bimanual reaches noted that participants tended to direct their gaze toward the right side of space, either in isolation or prior to making a leftward saccade (Honda, 1982). More recently, Riek et al. (2003) examined the direction of gaze during bimanual reaches to target pairs. They noted that participants tended to make two eye movements during symmetrical reaches: one from fixation and a terminal saccade toward the leftward target, indicating that the right side of space was monitored for the duration of the reach (see also Srinivasan and Martin, 2010).

Given that overt and covert attention can be readily dissociated (Posner, 1980; Hunt and Kingstone, 2003), it is quite possible that the direction of attention could be preferentially biased one way or the other without movements of the eyes. To this end, Baldauf and Deubel (2008) examined how a small number of right handers performed a simple perceptual task at the goal locations of a bimanual reach. They noted that, although perceptual performance was enhanced at the target locations for both hands, there were no differences in discrimination ability between the targets of the right versus the left hand. This lack of asymmetry may be due to a lack of power, but may also suggest that any attentional asymmetry might manifest itself in motor, rather than perceptual outcomes.

To examine motoric aspects of an attentional asymmetry, we have undertaken several experiments to using a discontinuous double-step bimanual reaching task (Buckingham and Carey, 2009). This task was adapted from classic double-step paradigms (Goodale et al., 1986), and consisted of two discrete steps: a bimanual reach toward a pair of visual targets followed by a unimanual reach to a new target which appeared halfway through the bimanual reach in 25% of the trials. Participants had to complete the bimanual reach before they made a unimanual reach with whichever hand was closest to the newly appearing single target. An asymmetrical allocation of attention during the bimanual reach should have behavioral consequences for the downtime between the bimanual and unimanual portions of the task (i.e., the refractory period). We predicted that participants would be able to prepare and commence the reaches with the attended hand more rapidly than with the non-attended hand, which would presumably require a time-consuming attentional shift in its direction prior to commencing the reach. In a sample of right-handed individuals we noted a clear advantage for the right hand, which was able to initiate the unimanual portion of the task some 20 ms faster than the left hand. This right hand advantage is particularly interesting because it contrasts the normal pattern of asymmetries observed during unimanual reaching tasks, where the left hand typically reacts faster than the right hand (Boulinguez et al., 2001). In other words, our data suggest that a right hand unimanual localization reaction time advantage only exists when preceded by a bimanual movement. Not only was this asymmetry reversed when participants were told to explicitly focus their attention toward their left hand during the task, but this attentional manipulation reduced the right hand's performance rather than improved the left hand's performance. These findings suggest (somewhat counterintuitively) that attending one's non-dominant hand may be a risky strategy for successful coordination of the hands.

To investigate how attentional biases may influence the propensity to select one hand over the other, we modified the double-step reaching task to include a hand selection cue (Bestelmeyer and Carey, 2004; Buckingham et al., 2011). As above, participants made a bimanual reach toward a pair of visual targets. Prior to this reach, however, they received a small vibratory cue to one of their hands to indicate which hand would have to perform the follow-up unimanual reach with 80% accuracy. The critical trials were when the cue was invalid (i.e., when the right hand was cued, but a left hand reach was required). Here, right-handed participants made more errors and a spent more time inhibiting the right hand when a left hand movement was required than the converse, suggesting that their right hand is pre-selected to undertake reaches. Left handers, by contrast, showed no such asymmetry, suggesting that they may lack any selection/attention bias whatsoever.

THE LINK BETWEEN ATTENTIONAL ASYMMETRIES AND MANUAL LATERALITY

The studies outlined above have indicated that subtle asymmetries which can be easily ascribed to attentional affects seem to favor (or be directed toward) the right hand of right handers. However, these findings offer little insight into the causal relationship between attentional and manual asymmetries. Clearly, altering one's hand preference is not simply a case overtly attending toward the non-dominant hand (Swinnen et al., 1996; Treffner and Turvey, 1996; Amazeen et al., 1997; Buckingham and Carey, 2009). It is, of course, also possible that attentional biases are a consequence, rather than the cause, of hand preferences. It is by examining attention and the emergence of manual laterality in a developmental context where the attentional bias hypothesis may succeed in breaking the cause and effect circularity which plagues theories of handedness.

The attentional bias hypothesis posits that attention is biased toward the right hand in a substantial proportion of the population from birth (Peters, 1981, 1991, 1994). This initial bias in attention may stem from the rightward orienting asymmetry which has been shown in human infants (Hopkins et al., 1987), and could lead to asymmetries in the roles assigned to either hand over the course of development. Continued use of the right hand as the performer of the more skilled portion of a dyadic task would then lead to inevitable right hand performance advantages as a function of practice. Little direct evidence for this causal link between attentional asymmetries and manual laterality exists, although there an increasing body of work indicating that attention can modulate the cortical underpinnings of motor learning, such as the generation of motor memories in primary motor cortex (Stefan et al., 2004). Furthermore, it is worth noting that infants are orientating their attention long before they are making purposeful movements, and some it has been established that the degree of rightward orienting bias seen in infancy does show a link to the development of manual asymmetries across childhood (Michel and Harkins, 1986). Indeed, a recent study has demonstrated that occluding the preferred arm of infants who have recently started reaching toward objects, results in a shift of their manual preference away from the occluded hand (Pogetti et al., 2014). However, longitudinal evidence for a link between attentionally modulated behavioral asymmetries during bimanual tasks in childhood and later-life unimanual hand preference would seem necessary to confirm the causal relationship between these factors.

While the link between consistent right hand selection and right hand performance advantages is easy to understand, it is worth considering why an attentional asymmetry is necessary in human motor coordination. Peters suggests that the key to the attentional bias hypothesis is bimanual coordination – the common factor linking the experiments described in this review. The 'kinematic chain' hypothesis, proposed by Guiard (1987) builds on the supposition that the majority of goal-directed actions are, to a degree, bimanual. In adults this bimanual coordination is often be symbolic or supportive in nature, with one hand facilitating the other's behavior (e.g., the left hand framing the face, while the right hand shaves with the razor blade). However, bimanual coordination is particularly prevalent in infancy where a combination of factors, such as a lack of motor skill and failure to inhibit mirror movements, ensures that bimanual interaction is the norm rather than the exception (for review, see Haywood et al., 2012). Developing from the simple reach-to-grasp behavior of infants to the complex goal-directed actions of adults, hand choice becomes a more complex matter of task assignment. One hand must be selected for a dominant role, whereas the other must be allocated a supporting role. It is this through the indirect link which an attentional asymmetry would drive adult handedness, linked by way of consistent selection biases which persist into unimanual variants of a multitude of tasks. Some tacit support for this proposition comes from Kourtis et al. (2014), who provided behavioral and electrophysiological evidence that performance in bimanual tasks with asymmetrical demands reflects the consistency, rather than the direction, of an individual's handedness.

Another point which is worth consideration is how to reconcile the rightward attentional bias which right handers exhibit during bimanual tasks with the oft-reported left hand unimanual reaction time advantage during unimanual localization tasks (Boulinguez et al., 2001), which may be related to right hemispheric attentional mechanisms that facilitate disengaging from fixation, or moving attentional resources toward suddenly appearing visual targets (Mieschke et al., 2001). Indeed, the attentional bias toward the right hand discussed throughout this review might seem counterintuitive, given the evidence for right hemispheric lateralization for attention in the human brain (Petersen and Posner, 2012). Separable mechanisms for attention (related to stimuli in the external world) and "intention" (or motor attention, related to selecting relevant and inhibiting irrelevant actions; e.g., Main and Carey, 2014) might go some way toward reconciling these viewpoints. For example, Rushworth et al. (2001) have found evidence suggesting that this motoric attention is not only independent from visuo-spatial attention, but appears to be lateralized to the opposite cerebral hemisphere.

ATTENTIONAL ALLOCATION IN LEFT HANDERS

Up until this point, only evidence has been presented from right-handed individuals. The situation for the understudied left handers remains unclear, largely because studies examining adextrals in this context are rare. In fact, they are crucial, if establishing the relationship to cerebral asymmetries is desired (see Carey and Johnstone, 2014, for review). In their study examining rhythmic coordination of the hands during synchronous pendulum swinging, Treffner and Turvey (1995, 1996) noted that left handers have the opposite pattern of asymmetries of right handers (i.e., a slight left hand phase lead, which is exacerbated at higher movement frequency). However, in Peters' (1981) bimanual tapping task and the cued bimanual reaching task of Buckingham et al. (2011), there was no clear evidence of any asymmetries. This does not mean that the left handers tended to perform equally well with both hands, but rather that there tended to be equally sized sub-groups who performed better with one hand (or configuration) than the other, canceling one another out. In other words, left handers appear to lack population-level asymmetry seen in right handers. Typically, across a variety of behavioral metrics, left handers tend not to be the mirror image of right handers (Bryden, 1982; Carey and Johnstone, 2014). Instead, left handers are typically more ambidextrous and variable in their hand preferences, with only a small proportion showing the same degree to asymmetries as right handers. Given the relatively non-asymmetrical nature of this population, left handers may be a subset of individuals who lack a rightward attentional bias, forming a Gaussian distribution around which hand they select for a particular task. With no external biases to select one hand over the other (although this point clearly is a contentious one in what is often described as a right-handed world) would lead the average 'unbiased' individual to select their left hand for half of the tasks they typically perform, and their right hand for the other half.

CONCLUSION

The underlying cause of human handedness is the cause of much debate. Here, we have presented the evidence for a bias in attention which occurs during bimanual coordination which may drive hand preferences, and presented a plausible account of how this bias would lead to manual asymmetries across the population. Future work on relating these effects to cerebral asymmetries in right and left handers, and how attentional and manual asymmetries develop and interact over developmental trajectories, may help clarify these relationships.

ACKNOWLEDGMENT

The authors would like to thank P. Dimitriou for his comments on an earlier version of the manuscript.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 03 October 2014; accepted: 24 December 2014; published online: 13 January 2015.

Citation: Buckingham G and Carey DP (2015) Attentional asymmetries – cause or consequence of human right handedness? Front. Psychol. ***5****:1587. doi: 10.3389/fpsyg.2014.01587*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 04 November 2014
doi: 10.3389/fpsyg.2014.01236

Aiming accuracy in preferred and non-preferred limbs: implications for programing models of motor control

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Most models of motor programing contend that one can perform learned actions with different muscle groups or limbs demonstrating the concept of motor equivalence. The goal of this review is to determine the generality of this concept within the context of aiming movements performed by both preferred and non-preferred limbs. Theoretical approaches to motor programing are described, followed by a comparison of a variety of kinematic measures taken from preferred and non-preferred limbs from simple and more complex aiming tasks. In general, the support for motor equivalency is strong for one- and two-dimensional aiming tasks and for simultaneous bimanual movements, but mixed for unconstrained throwing tasks and tasks that require feedback-based corrections.

Keywords: motor equivalence, motor programing, spatial accuracy, dominant and non-dominant limbs, temporal structure

One of the more persistent concepts of human motor control has been that of motor equivalence. The idea that one can achieve the same goal with different muscle groups or limbs has been proposed and described by several prominent researchers since the early 1900s (Head, 1920; Bartlett, 1932; Bernstein, 1967; Schmidt, 1975). Common examples include the ability of basketball players to shoot and dribble with either hand with equal proficiency, and for marked bilateral transfer in handwriting. At the same time there appear to be significant bilateral control differences between preferred and non-preferred limbs for a variety of motor tasks (e.g., Carson, 1989). Therefore, the goal of the present paper is to explore the concept of motor equivalency by investigating the differences between preferred and non-preferred limbs within the context of throwing and aiming movements in keeping with the topic on manual asymmetries, handedness, and motor performance. Theoretical approaches are described first, followed by sections describing the kinematic differences between preferred and non-preferred upper limbs in a variety of contexts (aiming movements and throwing) and experimental paradigms (adaptation studies and bimanual movements).

THEORETICAL APPROACHES

Bernstein (1967, p. 49) captured the idea of motor equivalence perfectly in the following quote:

> *It is clear that each of the variations of a movement (for example, drawing a circle large or small, directly in front of oneself or to one side, on a horizontal piece of paper or on a vertical blackboard) demands a quite different muscular formula; and even more that this, involves a completely different set of muscles in the action. The almost equal facility and accuracy with which all these variations can be performed is evidence for the fact that they are ultimately determined by one and the same directional engram in relation to which dimensions and position play a secondary role.*

For Bernstein, the engram was a central nervous system structure responsible for the control of both spatial and temporal movement characteristics. The engram controlled the entire movement, especially the order of the muscular contractions and the overall rhythm. These central features of the movement, which remained relatively constant from trial to trial, were termed topological characteristics and were controlled by the highest level of a hierarchical control system. At a lower level of the system, metrical characteristics (i.e., magnitude, muscle group) allowed for variations in expression of the engram and motor equivalency.

Schmidt (1975) made Bernstein's notions about the structure of the engram more explicit in the context of schema theory. According to the theory, motor equivalency was a result of the formation of a generalized motor program (GMP). The GMP was defined by so-called invariant characteristics that remained constant from performance to performance, but were different for different classes of movement (i.e., throwing, kicking). Schmidt (1975) identified relative timing, the sequence of events, and relative force as the invariant features of the GMP. Relative timing is defined as the proportion of the total time required by any phase of the movement (e.g., the proportion of total time taken by the stance phase in gait) and was thought to be invariant across changes in the overall movement time. Relative force is defined by the ratio of agonist/antagonist muscle activity, or by the relative magnitudes of flexion and extension movements, for example. The GMP is a flexible control structure because variable parameters could be used to change the movement outcome without requiring the use of a unique program. Overall duration, force, and muscle group were considered parameters that could all be varied across trials to change to outcome of the GMP. Therefore, the parameters are varied to change the magnitude of the movement from smaller to larger in the case of handwriting, or change the limb with which an object is thrown by changing the muscle group involved.

In the case of bilateral transfer, both the Bernstein's (1967) and Schmidt's (1975) ideas predict positive transfer because the same engram or GMP is used to control either limb. The invariant features would be preserved for use in both cases, while the parameters could be varied individually for each limb. However, the presence of manual asymmetries in the performance of the preferred and non-preferred limbs has required theoretical approaches involving the unique contribution of each cerebral hemisphere in the motor control process (Pan and van Gemmert, 2013).

For example, Hicks (1974) and Taylor and Heilman (1980) showed asymmetrical transfer such that the right hand benefited more than the left hand from opposite hand training. They proposed what has been referred to as an access model (Parlow and Kinsbourne, 1989) that states that a single motor program was stored in the left (dominant) hemisphere as a result of practice with either the preferred or non-preferred limb. The right hand benefits more than the left hand because the right hand has direct access to the information in the left hemisphere. The left hand has only indirect access to the information in the left hemisphere via the corpus callosum. The main limitations of the access model are that bilateral transfer is unidirectional and it cannot explain the results of studies showing that the left hand benefits more than the right from opposite hand training (e.g., Ammons and Ammons, 1951). As an alternative to the access model, Parlow and Kinsbourne (1989) proposed the so-called cross-activation model. In this case practice with the preferred limb creates motor programs in both the dominant and non-dominant hemispheres, although the program is weaker in the non-dominant hemisphere. Training only the non-dominant hemisphere only creates a motor program in the non-dominant hemisphere. According to this model bilateral transfer is always stronger from the preferred limb to the non-preferred limb than vice verse due to the lack of a motor program in the dominant hemisphere after non-preferred limb practice. As with the access model, only transfer from the preferred to the non-preferred limb can be explained. More recently Sainburg and colleagues (Sainburg and Wang, 2002; Wang and Sainburg, 2004, 2006) have argued that the preferred and non-preferred hands have access to all the information learned by the opposite hand, but controllers unique to each hand select and use information differently. For example, the dominant hemisphere mechanisms underlie specification of the shape and direction of the movement trajectory, while the non-dominant hemisphere specializes in final limb position.

MOTOR EQUIVALENCY IN AIMING MOVEMENTS

One way to organize the vast amount of information on aiming movements is to first describe the differences between preferred and non-preferred limbs in the simplest tasks involving one- and two-dimensional movements, followed by work on unconstrained three-dimensional movements. If the concept of motor equivalency is truly a general one, then evidence should be available for all aiming tasks.

Perhaps the simplest aiming movement studied involves moving a lever or joystick so a cursor reaches a target displayed on a computer screen. Spatial errors can only be made in the single dimension of distance, and movement time can be controlled with instructions and augmented feedback. On such study was performed by Zuoza et al. (2009) in right-handed male participants, where the goal was to move a joystick "quickly and accurately" so the cursor reached the target in 400–600 ms without concurrent visual feedback. The preferred limb was more accurate than the non-preferred limb, although when errors were made the preferred limb tended to undershoot the target and the non-preferred limb tended to overshoot the target. In absolute measures, the non-preferred limb spent less time in deceleration than the preferred limb and showed greater peak and average velocity than the preferred limb as well. However, such differences could simply be attributed to changes in parameters of the GMP as discussed earlier. The preferred limb spent 42 and 58% of the total time in the acceleration and deceleration phases, respectively, compared with 45 and 55% for the non-preferred limb, suggesting a very similar relative timing pattern for both limbs. In another study, participants moved a lever in the horizontal plane different distances (5°, 10°, 20°, 30°, and 40°) with each arm at a self-selected speed (Al-Senawi and Cooke, 1985). There was no difference in spatial error between the limbs and the velocity profiles were nearly identical as well. These results support the GMP explanation for motor equivalency since it is likely the same motor program was used for the control of both limbs. In addition, the Al-Senawi and Cooke (1985) study supports Bernstein's notion about the facility of transfer between the limbs.

Two-dimensional aiming tasks are typically done on digitizing tablets or other surfaces using a computer mouse where the target is displayed on the testing surface or on the computer screen. Errors can be made in the horizontal and/or vertical planes and concurrent visual feedback can be provided or limited. In one study, Sainburg and Kalakanis (2000) participants moved to targets requiring 20° of elbow excursion and either 5°, 10°, or 15° of shoulder excursion without concurrent visual feedback with both preferred and non-preferred limbs. Target accuracy, and elbow and shoulder joint angles were computed for both limbs. Unlike one-dimensional aiming tasks, the hand paths were highly curvilinear with the left hand showing a "left to right" path and the right hand a "right to left" path, but target accuracy was the same in both limbs. Although relative timing was not computed, the ratio of shoulder to elbow excursion was computed for each target condition. The shoulder/elbow ratio taken at the peak velocity was greater for the right hand compared to the left hand, but no difference in the ratio was detected at the final target position. An analysis of the joint torques indicated that each limb to achieve the target used different strategies. The right arm used elbow and shoulder torques synergistically to move the upper arm while the same torques countered one another in the left arm. Overall, the evidence here suggests that different GMPs were used to control the two limbs, although accuracy was equal for both limbs.

The two studies reviewed thus far showed mixed results in terms of motor equivalency when movements were made without the benefit of concurrent visual feedback. Would motor equivalency be shown if visual feedback was available for both limbs? Carson et al. (1993) studied the accuracy and kinematic pattern of aiming movements with various levels of concurrent visual feedback available. Participants had full vision of the arm and target, or just the target, or just the arm, or neither the arm nor target in different conditions. Instructions were also given to be either fast or accurate. The right-handed participants were more accurate with the right hand compared with their left hand across all visual conditions. Although relative timing was not presented, the percentage of time before and after peak velocity could be calculated from the data presented. Under the fast movement instruction 30 and 70% of the total time were spent before and after peak velocity, respectively. Somewhat greater relative time was spent after peak velocity (73.6%) when accuracy was emphasized. However, the relative timing pattern in the left and right limbs was nearly identical across all visual feedback conditions suggesting that the same GMP was used to control both limbs. This finding was supported by Bryden (2002) in a study using Fitts' paradigm where the index of difficulty (ID) varied from 3.06 to 14.29 bits of information. As predicted by Fitts' law, movement time increased directly with ID for both the left and right arms. However, there was no difference between the arms on any kinematic measure of performance including the relative time spent in acceleration or deceleration, again supporting the notion of motor equivalency.

Perhaps the most effective test of the concept of motor equivalency is when a metrical characteristic like distance or time is varied and the relative timing structure is compared across limbs. Poston et al. (2009) varied the required angle of aiming movements (either 5°, 45°, or 85°) to the left and right of the participant's midline. Movements were made until the target was contacted, so spatial errors were essentially 0. Analysis of the kinematics revealed that the movement time, average velocity, the relative length and duration of the primary submovement, and the normalized jerk were nearly identical in both limbs. These results suggest that the same GMP was used for both limbs due to the very similar relative timing patterns in both limbs. Sainburg and Schaefer (2004) varied movement distance (10°, 20°, 35°, and 45°) requiring "uncorrected" elbow extensions in both limbs. There were no interlimb differences in spatial accuracy, but somewhat different kinematic patterns were shown between the limbs. In both limbs, peak velocity and the time to peak velocity scaled directly with distance, although the slope of the time to peak velocity/distance relation was greater for the non-preferred limb. Also, the acceleration-time patterns were different. In the non-preferred limb, the initial peak in acceleration was nearly constant across distances, with additional positive peaks emerging during the movement. The initial peak in acceleration scaled directly with distance in the preferred limb. These results suggest that different motor programs were used whereby distance was varied in the non-preferred limb by changing the duration of the acceleration-time pulse, while the preferred limb varied the amplitude of the acceleration-time pulse (cf., Brown and Cooke, 1984; Ghez and Gordon, 1987). It could be that the strategy used by the preferred limb was due to extensive practice dedicated to that limb, and the strategy used by the non-preferred limb could be indicative of relatively novice performance. Roy et al. (1994) instructed participants to make either "fast" or "accurate" movements to targets and showed a very similar relative timing pattern in the left and right limbs in both fast and accurate instructional conditions. However, much less relative time was devoted to the time after peak velocity (55%) in the speed condition compared with the accurate condition (72%), suggesting that a different GMP was used in the two conditions.

One advantage of using two-dimensional aiming movements to investigate the concept of motor equivalence is that the relative timing pattern could be easily determined because the participant decelerates the limb when approaching the target. The case is different when evaluating the relative timing pattern in unconstrained three-dimensional aiming movements, because the pattern of deceleration could be disrupted by the impact of the limb with the target surface. This problem was highlighted by Todor and Cisneros (1985) who investigated the accuracy of aiming movements using a "dart-throwing" motion over 40.64 cm to targets 0.635, 1.27, or 2.54 cm in diameter. Four phases of the acceleration-time trace were identified: T1, time to peak positive acceleration, T2, time from peak positive acceleration to zero acceleration, T3, time from zero acceleration to peak deceleration, and T4, time from peak deceleration to target contact. Trials were classified based on the duration of T4. Trials were labeled "late" if T4 was less than 50 ms, or "early" if T4 was greater than 50 ms. The average T4 duration of the late trials was less than 5 ms, indicating that peak deceleration occurred immediately before target impact. The duration of T4 in the early trials was greater than 100 ms, indicating that the participants were able to slow the limb down to some extent before target impact. Focusing only on the early trials, the relative timing pattern involving T1, T2, and T3 were very similar for the left and right hands suggesting initial use of the same GMP. However, the left hand spent 4% more relative time in T4 on average compared with the right hand, suggesting the left hand required more time to make movement adjustments when approaching the target. Haaland and Harrington (1989) replicated these results by showing similar relative timing for the left hand and right hand for the initial (LH = 53.5%, RH = 51.2%) and corrective (LH = 46.4%, RH = 48.7%) movement phases using the Fitts' paradigm. Further support for motor equivalency was provided by Barral and Debû (2004) similar proportions of time in the decelerative phase for both limbs for three different target locations in women. In men, the relative timing was the same for two of the three target locations.

MOTOR EQUIVALENCE IN THROWING

There was clear evidence for motor equivalence in laboratory-based aiming tasks performed with both left and right limbs. The relative timing pattern based on velocity or acceleration-time records was very similar for both limbs in most circumstances. This section reviews studies comparing the preferred and non-preferred limbs in throwing, arguably the least constrained aiming task possible. McDonald et al. (1989) investigated kinematic differences between left and right limbs in dart-throwing in well-practiced participants (500 practice trials for the preferred hand, 1250 for the non-preferred hand). Wrist, elbow, and shoulder joint angles were calculated for the first and last 10 throws for each limb. Accuracy was better in the preferred limb compared with the non-preferred limb, although accuracy improved in both limbs over the practice trials. Within-limb correlations between joints for angular displacement and angular velocity tended to be higher for the non-preferred limb compared with the preferred limb. However, there were strong correlations between the preferred and non-preferred limbs for the resultant displacement and the resultant velocity (all above 0.83) suggesting the same kinematic pattern was shown by both limbs. However, the relative timing pattern was not described in the study nor were data available to calculate the appropriate percentages, so the degree of motor equivalence could not be determined.

Along the same lines, Hore et al. (1996) provided a kinematic analysis of preferred and non-preferred limbs is a seated throwing task. The timing and velocity of proximal joints (shoulder, elbow, and wrist) and distal joints (fingers) were measured and correlated with target accuracy. Target accuracy was better in the preferred limb than the non-preferred limb, and joint rotations were more variable in the non-preferred limb compared to the preferred limb. However, the hand path trajectories were very similar between the left and right arms for a given participant. Different participants showed quite varied "styles" of throwing. Again, the relative timing pattern for each limb was not provided. In a more recent study, Hore et al. (2005), participants threw baseballs at a target at three different speeds with both preferred and non-preferred limbs. Throws with the preferred limb were different from the non-preferred limb in several respects. For preferred limb throws, the joint positions at ball release were different across speeds for the elbow, wrist and shoulder. In addition, participants varied the coordination between joints to achieve throws of different speed. The evidence for a similar relative timing pattern was mixed. There was no evidence for consistent relative timing of elbow, wrist, and shoulder positions across speeds, but there was some evidence for a similar relative timing pattern of the vertical component of the hand path across throwing speeds, but only for the preferred limb. Throws with the non-preferred limb showed relatively small differences in joint motions across speeds compared with the preferred limb. For example, there were no differences in wrist, elbow, or shoulder position at ball release across speed. Further, there was little evidence for a consistent relative timing in the non-preferred limb.

The study by Hore et al. (2005) has some interesting implications for the concept of motor equivalency. Skilled throwers apparently vary the joint coordination pattern in order to change ball speed to accomplish changes in velocity for the preferred limb. However, when learning to throw with the non-preferred limb, they initially use a very similar spatial pattern suggesting they use the same GMP across changes in speed. Also, in a complex coordination task like throwing, the evidence for a consistent relative timing is mixed, and depends on what movement characteristic is evaluated and the throwing limb. The relative timing of some aspects of the hand path and finger opening (Hore and Watts, 2005) are maintained across speeds, but not for elbow, wrist, and shoulder positions.

ADAPTATION STUDIES

Another experimental design that could be used to evaluate motor equivalency is a design where practice is first provided for either the preferred or non-preferred limb under normal target conditions, and then the same or opposite limb is tested when the target is displaced or visual feedback is rotated, for example. In the study by Sainburg and Wang (2002), participants moved to one of eight targets with goal movement times between 400 and 600 ms, beginning with either the left or right limb. After baseline trials under normal visual feedback conditions, the cursor was rotated 30° relative to the start position and practice continued with the opposite limb. The amount of bilateral transfer depended on what kind of error was evaluated. For direction error at peak velocity, the right arm benefited from left arm training, but the left arm did not benefit from right arm training. However, the left arm did benefit from right arm training for end position error, but not the right arm. These results support the dynamic dominance hypothesis that holds that preferred hemisphere mechanisms underlie specification of the shape and direction of the movement trajectory, while the dominant hemisphere specializes in final limb position (Wang and Sainburg, 2004, 2006). However, the study did not provide information on relative timing so the concept of motor equivalency could not be evaluated completely. One study that was somewhat more relevant for evaluating motor equivalency was performed by Pan and van Gemmert (2013). They had right-handed participants make movements on a digitizing tablet to four targets in four directions beginning with their left or right hands. After practice under normal visual feedback conditions, the feedback was rotated 45° and practice was provided either the left or the right hand. As in the Sainburg and Wang's (2002) study, asymmetric transfer was shown. Practicing with the right hand under rotated visual feedback conditions showed positive transfer to the unpracticed left hand as reduced movement time, trajectory length, normalized jerk, and initial direction error. The ratio of the primary submovement to the total time and the length from the primary submovement to the target also showed transfer effects. However, practice with the left hand under rotated feedback conditions only showed transfer to the right hand for movement time, trajectory length, and normalized jerk. Apparently, the relative timing pattern learned by the right hand was utilized by the left hand, supporting the concept of motor equivalency, but not for the opposite direction.

MOTOR EQUIVALENCY IN BIMANUAL MOVEMENTS

Next, we turn to the work on simultaneous bimanual movements when both limbs make aiming movements to either the same or different targets at the same time. In their first experiment, Kelso et al. (1983) kinematic analyses of bimanual aiming movements using Fitts' (1954) task where participants made movements to combinations of easy (target width, W = 7.2 cm, distance, A = 6 cm, ID = 0.74) and hard (W = 3.6 cm, A = 24 cm, ID = 3.74) targets. When both hands moved to similar targets, the average interlimb difference in movement time was 6 ms. When the hands moved to targets of different difficulty the average movement time difference was 23 ms. Regardless of the bimanual condition (easy–easy, hard–hard, easy–hard) the time of peak velocity and the time of maximum vertical displacement were very similar for both limbs. Although the relative timing of the kinematic patterns was not provided, when referring to the easy–hard movement condition they reported, "although the paths of the two trajectories are obviously different, their form looks remarkably alike as if one were an expanded (or contracted) version of the other." Their second experiment also supported the notion that both limbs were controlled by the same motor program when a hurdle was placed in the path of one of the hands as both hands moved to hard targets. Most participants showed spatially symmetrical movements in both hands even though only one hand was required to clear the hurdle, while three subjects showed relatively independent movements in each hand. Fowler et al. (1991) replicated Kelso et al.'s (1983) work and added a more difficult target condition (W = 2 cm, A = 36 cm, ID = 5.17). When the 0.74 ID and 3.74 ID movements were combined the movement time differences were 33 ms, and 57 ms when the 0.74 ID and 5.17 ID were combined. Analysis of the resultant velocity and acceleration indicated that participants were very consistent within and between testing conditions, particularly when moving to the same target in each hand. When different targets were involved, greater between-subject variation was noted. Some participants showed a high degree of synchronization, while others showed a lack of synchronization. In general, moving to different targets caused interlimb differences in the form of the velocity-time curve depending on which hand moved to the harder target. However, the relative timing of the various peaks in velocity and acceleration were not computed so the implication for motor equivalency could not be determined.

However, Sherwood (1994) examined the relative timing in simultaneous bimanual aiming movements involving the same or different distances in each hand. The right hand goal was always 60°, and the left hand moved either 30°, 40°, 50°, or 60°. As expected, the left hand overshot the 30° and 40° targets and the right hand undershot the 60° target showing assimilation effects. However, an analysis of the relative timing of three landmarks (time of peak positive velocity, the time of the intermediate zero crossing, and the time of peak negative velocity) were very similar for the left hand (31, 51, and 75%) compared with the right hand (29, 51, and 75%). Clearly over changes in distance the same GMP controlled each hand.

More recently, Maslovat et al. (2008) provided an interesting test of motor equivalence by contrasting bimanual movements initiated by a control tone (82 dB) or a startle tone (124 dB) where the left hand goal was 10° and the right hand goal was 20° of elbow extension. The endpoint error was greater in the left hand compared with the right hand, particularly on the startle trials. As expected the premotor reaction time was reduced by about 50% on the startle trials relative to the control trials. However, the velocity profiles were strongly correlated across limbs (all above 0.90) for both control and startle trials. Also, this study provided an excellent analysis of the electromyographic (EMG) pattern underlying the control and startle trials. They recorded surface EMG from the left and right triceps brachii and biceps brachii, and the left sternocleidomastoid muscles on control and startle trials. On both startle and control trials the expected triphasic EMG pattern was shown in both limbs with a single burst of antagonist activity appearing between the two agonist bursts. The onset and offset times of the agonist and antagonist muscles were invariant across limbs and conditions, strongly supporting the concept of motor equivalency. Interestingly, sternocleidomastoid muscle activity was only shown on the startle trials and its activity preceded the agonist muscle activity by an average of 50 ms.

SUMMARY: FACTORS INFLUENCING MOTOR EQUIVALENCY

The evidence for motor equivalency presented in the previous sections was clearly mixed with studies showing evidence both for and against the concept. The goal for this section is to identify general factors that influence the presence of motor equivalency. One factor that has a strong influence on motor equivalency is the task involved. Evidence for motor equivalency is strong when one- or two-dimensional movements are made to predicable target locations (Poston et al., 2009; Zuoza et al., 2009). Because of the stable environmental conditions the GMP can be prepared in advance and run without a concern for online corrections. The learned invariant characteristics of the GMP can be easily applied to the both limbs by simply changing the muscle group used for the task. The importance of preprograming was also emphasized by the work of Maslovat et al. (2008) when rapid movements were produced by triphasic EMG patterns of both limbs when activated by startle responses.

The second task type to show strong evidence for motor equivalency was when simultaneous bimanual movements were made to either the same of different targets. According to models of bimanual control (Marteniuk and MacKenzie, 1980; Marteniuk et al., 1984), the same GMP is used to control both limbs, but different parameters could be assigned to each limb if needed. If both limbs need to travel the same distance or move to the same sized targets, the same level of force or amplitude could be applied to both limbs. But, if different distances are required, then different levels of force could be applied to the each limb independently. In both cases, the invariant features of the GMP should be preserved in each limb. The reviewed studies by Sherwood (1994) and Maslovat et al. (2008) clearly support the concept of motor equivalency in bimanual movements.

Mixed support for motor equivalency was shown when movement corrections were required in order to reach the target. Carson et al. (1993) showed that more relative time was required during the decelerative phase compared with the accelerative phase, but this pattern was the same for both preferred and non-preferred limbs. On the other hand, when participants have to adapt to new visual feedback conditions when the target location is rotated, the amount of transfer depends on the order of practice. Pan and van Gemmert (2013) showed that the relative timing pattern learned by the right hand was used by the left hand, but not for the opposite direction. It could be that additional practice was required by the left hand in order to attain motor equivalency.

The least amount of support for the concept of motor equivalency comes from unconstrained tasks like three-dimensional aiming and throwing, but for different reasons. In three-dimensional aiming tasks, the relative timing pattern in deceleration is frequently disrupted by target impact (Todor and Cisneros, 1985), so many practice trials cannot be used for analysis. But, when the relative timing of both accelerative and decelerative phases were available for analysis, the support for consistent relative timing and motor equivalency were shown (Haaland and Harrington, 1989). As for throwing tasks, several studies did not report relative timing measures so the concept of motor equivalency could not be determined (e.g., Hore et al., 1996). However, the Hore et al.'s (2005) study reported some evidence for a consistent relative timing in the preferred limb but not in the non-preferred limb.

A second major factor determining whether support is shown for motor equivalency is the measures that are taken. Motor equivalency is evaluated on the basis on relative time or relative force measures, but several of the studies in this review did not report relative timing measures, but still provided important information on bilateral transfer. For example, Sainburg and Kalakanis (2000) provided an analysis of joint torques and relative joint motions for both the left and right hands instead of relative timing measures. Their work suggested that the limbs were controlled by different GMPs, but without relative timing measures the conclusions were not definitive. If the concept of the GMP is expanded to include measures like relative joint motions then this type of work would be more relevant for the concept of motor equivalency.

Finally, practice likely has an important role in establishing the GMP in the non-preferred limb, particularly in unconstrained throwing tasks. McDonald et al. (1989) provided 1250 practice throws for the non-preferred limb and showed strong correspondence between kinematic patterns of both limbs, suggesting that considerable practice was required before motor equivalency could be attained.

RECONCILING MOTOR EQUIVALENCY AND ASYMMETRICAL BILATERAL TRANSFER

As noted at the beginning of the paper, one of the challenges for the concept of motor equivalency was the notion that each hemisphere contributes differently to the motor control process. In a majority of the studies reviewed, the accuracy of the preferred and non-preferred limbs were equivalent, supporting Bernstein's notion that the same motor program could easily be used to control both limbs. However, in most of these studies, errors could only be made in one dimension. In studies where direction error could be dissociated from final position error, it has been shown that the left (preferred) hemisphere provides the shape and the direction of the movement, while the right (non-preferred) hemisphere specializes in final limb position (Sainburg and Wang, 2002; Wang and Sainburg, 2004, 2006). It could be that a GMP is available for the control for either limb, but depending on the task requirements, the program could be adapted to fit the situation. If the GMP can carry out the task without need of movement corrections, then the program can be applied to both limbs expressing motor equivalency. If movement corrections are needed to attain the target, then the right hemisphere can become active to initiate the corrective process that would minimize the influence of the original GMP. Secondly, the GMP could specify the relative timing structure of movements with either limb, but manual asymmetries could emerge due to differences in the parameter specification process undertaken at a lower level of the control system. This notion could account for reduced movement variability and more precise force production in the preferred limb relative to the non-preferred limb (Annett et al., 1979; Peters, 1980).

LIMITATIONS ON THE WORK IN MOTOR EQUIVALENCY AND FUTURE DIRECTIONS

Even though many studies have been conducted on bilateral transfer and motor equivalency in aiming movements, some limitations in the work should be recognized. For example, the finding supporting the concept of motor equivalency in studies on bilateral transfer crucially depend on how the preferred and non-preferred limbs are compared. In most studies reviewed in this paper, the limbs are compared after significant practice has occurred in both limbs (cf., McDonald et al., 1989). In this situation, it is not surprising that the non-preferred limb mirrors the characteristics of the preferred limb, or vice versa. Perhaps the ultimate test of the concept of motor equivalency would be to examine the invariant characteristics of the non-preferred limb on the initial practice trials following extensive practice with the preferred limb. Future work could establish the amount of transfer in this and other contexts (Robinson et al., 2010).

A second limitation of the current work on motor equivalence is the dependence on mean scores for relative timing and accuracy, for example. In many of the reviewed studies, the relative timing pattern for the preferred and non-preferred limbs were very similar, and not significantly different. However, the analysis of the mean scores ignores individual differences. Strong evidence for motor equivalency should be reflected in positive within-subject correlations in invariant characteristics it addition to similar means. However, such correlations are reported infrequently (McDonald et al., 1989 is an exception) so future work could establish the strength of the coordination between limbs. Also, it is quite likely that some performers would show greater evidence for motor equivalency than others based on factors such as past motoric experience, movement efficiency, genetics, strategies, or in general, intrinsic dynamics (Kelso, 1999). Perhaps future studies could follow the lead of Kelso et al. (1983) and Fowler et al. (1991) whom reported individual differences in bimanual coordination of aiming responses, for example.

Finally, the assumption that movement kinematics are a direct result of the GMP could be called into question. For example, the kinematic pattern of aiming movements, regardless of limb, could be a function of efficiency rather than specified by the program. As accuracy demands increase, performers spend more time in the deceleration phase (Carson et al., 1993) perhaps to use more efficient feedback-based processing than central control. Future studies could evaluate movement efficiency using EMG, for example, to help distinguish between the GMP and efficiency explanations for the kinematic pattern in aiming movements.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 28 August 2014; accepted: 10 October 2014; published online: 04 November 2014.

*Citation: Sherwood DE (2014) Aiming accuracy in preferred and non-preferred limbs: implications for programing models of motor control. Front. Psychol. **5**:1236. doi: 10.3389/fpsyg.2014.01236*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 04 December 2014
doi: 10.3389/fpsyg.2014.01406

Modulation of manual preference induced by lateralized practice diffuses over distinct motor tasks: age-related effects

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In this study we investigated the effect of use of the non-preferred left hand to practice different motor tasks on manual preference in children and adults. Manual preference was evaluated before, immediately after and 20 days following practice. Evaluation was made with tasks of distinct levels of complexity requiring reaching and manipulation of cards at different eccentricities in the workspace. Results showed that left hand use in adults induced increased preference of that hand at the central position when performing the simple task, while left hand use by the children induced increased preference of the left hand at the rightmost positions in the performance of the complex task. These effects were retained over the rest period following practice. Kinematic analysis showed that left hand use during practice did not lead to modification of intermanual performance asymmetry. These results indicate that modulation of manual preference was a consequence of higher frequency of use of the left hand during practice rather than of change in motor performance. Findings presented here support the conceptualization that confidence on successful performance when using a particular limb generates a bias in hand selection, which diffuses over distinct motor tasks.

Keywords: handedness, non-preferred hand use, right-handers, diffusion of manual preference, confidence

INTRODUCTION

Human laterality has been understood traditionally from the perspective that there is a dominant hemisphere for motor control, leading to intermanual performance asymmetry favoring the dominant hand (Annett, 1972; Levy and Nagylaki, 1972; McManus, 1985). Based on intermanual performance asymmetry, a lateral bias of use is established with the dominant hand becoming the preferred one to perform motor actions in general. From this perspective, manual preference to perform voluntary movements is expected to be a stable characteristic of motor behavior. However, contradictory to the expectation of stability of manual preference, different investigations have shown that the relative frequency of use of the right/left hand is malleable, and that it depends on lateralized experiences. Malleability and generalization of manual preference as a result of lateralized motor experiences have been investigated through experimental approaches in children and adults. Teixeira and Teixeira (2007) provided right-handed adults with practice for the non-preferred left hand in sequential touches between the fingers and the thumb, assessing variation of manual preference afterwards. Evaluation of manual preference revealed that 7 out of 10 participants shifted from right to left hand preference to perform the specific experimental task immediately after practice. More specifically, at that moment four participants declared that, if they had opportunity to choose, they would select exclusively their left hand to perform the experimental task, and three other participants would use their left hand in most trials. Thus, practice with the left hand in the experimental task created a specific manual preference incongruent with the global preference for the right hand to perform daily living motor tasks. That effect was retained over 1 month of rest, showing to be a persistent one. An additional point of interest in those results was that no correlation was found between manual preference and intermanual performance asymmetry. In fact, there were some cases of contradictory relationship between manual preference and performance asymmetry. In a follow-up experiment, Teixeira and Okazaki (2007) evaluated the extent to which lateralized practice induces modulation of manual preference not only for the specifically practiced task but also for distinct motor tasks. To evaluate generalizability of modulation of manual preference by lateralized practice, we provided adult right-handers with practice of a single sequence of fingers movements using their non-preferred left hand, and assessed its effect on manual preference for two other sequences of fingers movements. Results revealed that repeated use of the non-preferred left hand during practice led to modulation of manual preference both for the specific task and for another one having the same sequential structure as that practiced. Similarly to what was observed for the practiced task, the effect of generalization was persistent over time. Of particular interest, analysis of movement time revealed that practice with the non-preferred hand led to similar performance gains between the hands. Therefore, shift of manual preference was not associated with intermanual performance asymmetry.

Results from these two experiments revealed the malleability of manual preference even in right-handed adults, an age group having stable manual preference in daily living tasks, and that modulation of manual preference induced by unimanual practice of one task can affect manual preference in distinct motor tasks.

To assess the extent to which use of a single hand in daily living activities is able to bias manual preference in non-practiced tasks, we (Teixeira et al., 2010) provided 3- and 4-year-old children with motor experiences with their non-preferred left hand in different tasks requiring pencil manipulation. Manual preference was probed by evaluating the hand chosen to perform a simple task of reaching and grasping a pencil, and a complex task requiring reaching, grasping and inserting the pencil into a small orifice. Grasping targets were positioned at the midline and at different eccentricities in both sides of the child's workspace. As expected, before practice the children showed a noticeable preference for using their right hand, particularly when reaching for targets positioned at the midline and at different points of the right hemispace. Following practice, the children manifested higher rates of use of the left hand at the midline and at right-sided target positions. Modulation of manual preference was expressed through prevalent use of the left hand across target positions, or lower frequency of use of the right hand in comparison with the pretest. That effect was observed for both the simple and complex motor tasks. From these findings, we forged the concept of "diffusion of manual preference" to convey the notion that a lateral bias developed by predominant use of a single hand to perform one or a group of motor actions spreads over other tasks having similar movement control requirements.

This series of experiments oriented to understand the effect of systematic use of a single hand on manual preference suggest that shift of manual preference following practice is not necessarily associated with an improved status of the non-preferred hand in intermanual performance asymmetry. It might be thought from the findings of modulation of manual preference by use that hand selection is biased by the confidence one acquires that successful performance can be achieved with a particular hand based on its history of use. Support for this conceptualization has been provided by Stoloff et al. (2011) through manipulation of the perceived rate of success in the performance of an aiming task with the preferred or non-preferred hands. In this experiment, they increased the probability that trials performed with the non-preferred hand received feedback indicating successful performance, and did the opposite to performance with the preferred hand by increasing the frequency of sense of failure when using that hand. This procedure induced a higher proportion of use of the non-preferred left hand, an effect that persisted following the end of feedback manipulation. Participants reported to be concerned regarding performance with their non-preferred hand at the experiment onset, whereas they declared to have become confident on using that hand over trials. Additionally, most participants declared that the task seemed to have become easier to be performed with their left hand across trials. These results support the conjecture that confidence achieved by hands use modulates manual preference to perform motor actions.

In the present experiment, we evaluated the extent to which higher frequency of use of the non-preferred hand in several motor tasks modulates manual preference in different probing tasks. For this evaluation, in addition to adults, we assessed 8- to 10-years-old children because this age has been shown to be associated with the most consistent use of the preferred right hand (Bryden and Roy, 2006; Doyen et al., 2008; Hill and Khanem, 2009). By selecting these age groups, we aimed at making a strict test of the effect of lateralized practice on manual preference by using participants who can be considered to be the most difficult ones to induce increased use of the non-preferred hand. Manual preference was probed by using targets arranged at different points in the left and right sides in egocentric coordinates of the workspace (cf. Bishop et al., 1996). This setup has proved to provide a discriminant assessment of consistency of manual preference, since right-handers have been observed to use their preferred hand consistently to reach for targets placed either at the midline position or in the right hemispace, whereas targets positioned in the left hemispace induce increased use of the left hand as eccentricity of target position is increased. This effect has been observed in children (Gabbard et al., 2001; Leconte and Fagard, 2004, 2006; Bryden and Roy, 2006; Carlier et al., 2006; Doyen et al., 2008; Hill and Khanem, 2009), as well as in adults (Bishop et al., 1996; Bryden et al., 2000; Stins et al., 2001; Bryden and Roy, 2006). To increase the discrimination power of the evaluation of manual preference, we also compared tasks of different complexities. Complex tasks have been shown to lead to higher frequency of use of the preferred hand both in children (Rostoft et al., 2002; Fagard and Lockman, 2005; Mayer and Bryden, 2008; Hill and Khanem, 2009) and in adults (Calvert and Bishop, 1998; Mamolo et al., 2004). Thus, it is expected that manual preference in complex tasks is less amenable to modulation by hands use than in simple tasks. An additional point of original interest in the present investigation was evaluation of manual preference in parallel with analysis of movement kinematics, in order to acquire further insight into the role of intermanual performance asymmetry in hand selection. Considering that the practice tasks were different from those evaluated and that there was no emphasis on performance improvement during practice, we expected to find no modification of intermanual performance asymmetry resulting from practice. Based on the concept of diffusion of manual preference, we hypothesized that practice of different motor tasks using the non-preferred hand induces increased preference of that hand to perform distinct motor tasks.

MATERIALS AND METHODS

PARTICIPANTS

Eighteen children ($n = 9$ for each gender), age range 8–10 years old ($M = 9.2$ years, $SD = 0.6$), and 18 adults (females $n = 11$, males $n = 7$), age range 18–28 years old ($M = 22.5$ years, $SD = 3.1$), volunteered for this study. Participants self-declared to be right-handed for handwriting and for daily living manual tasks. In addition, children had right-handedness confirmed by the respective teacher or parent. Adults and children's parents signed an informed consent form, as approved by the local university ethics committee.

TASK AND EQUIPMENT

For probing manual preference we used two tasks differing in complexity[1]. The simple task consisted of reaching, grasping and laying down cards arranged at different eccentricities in the workspace on a supporting half-moon shaped table. Paper cards (8.5 × 5 cm) were supported in vertical orientation by cardholders at seven positions regarding participants' egocentric coordinates. Card positions were midline, three positions in the left side, and three positions in the right side. Cards were placed on an imaginary semicircle, 25 cm far from the proximal border of the table, with 30° spacing between adjacent cards (approximately 25 cm of linear distance). Those positions were numbered from 1 to 7, leftmost and rightmost respectively, with the number 4 corresponding to the midline position (**Figure 1**). In the complex task, participants were to grasp the card, transport and insert it into a slot. The slot was 6-cm long, 3-mm wide, being oriented parallel to participants' frontal plane. It was located 12 cm away from the table's proximal border, at the midline position. Initial position for the hands was on the participant's lap, supporting each hand on the ipsilateral leg. Adults were sat at a regular chair keeping their hip and knees flexed at 90° approximately, while children were sat at a height adjustable chair, keeping the same position as described for the adults.

For motor performance assessment, we used a modified version of the complex task. For this task, the card was placed at the central position, 20 cm far from the slot. Initial position was supporting the active hand on the table, 30 cm far from the card, near the proximal border of the table, aligned with the central position. The index finger and thumb were kept touching each other, with the hand oriented in a comfortable neutral position. Participants were to use their index finger and thumb in a pinch-like movement to pick up the card, making contact with the card at its upper border. For kinematic analysis, reflective markers were attached to the participants' index finger and thumb nails, and to the center of the radiocarpal joint of both hands. Four opto-electronic cameras (MX3+, Vicon) were used for acquisition of kinematic data.

[1]The term "complexity" is used here to denote use of attentional resources due to accuracy demand of the task.

EXPERIMENTAL DESIGN AND PROCEDURES

The experiment was conducted in four phases: pretest, practice, posttest, and retention. In the pretest, we assessed manual preference and performance asymmetry for the simple and complex tasks. Evaluation of manual preference was made through sets of 7 trials, one trial for each card position within a set. Manual preference for each task complexity was assessed through four sets of trials, corresponding to four trials for each card position, as it has become standard from previous investigation (Souza et al., 2012; Pogetti et al., 2014). In total, participants performed 28 trials for each task complexity. Sequence of card positions was pseudorandomized in each set of trials, with the card to be grasped being indicated by the experimenter through verbal instruction. Movements were self-paced following a command to initiate a trial. Participants were informed that they could freely select the right or the left hand to perform the tasks. Intertrial intervals within a set of trials were approximately 10-s long, and intervals between sets of trials were approximately 30-s long. For evaluation of motor performance, participants performed four trials of the modified complex task with each hand. Sequence of task complexities and hands were counterbalanced within each group (see groups description in the following).

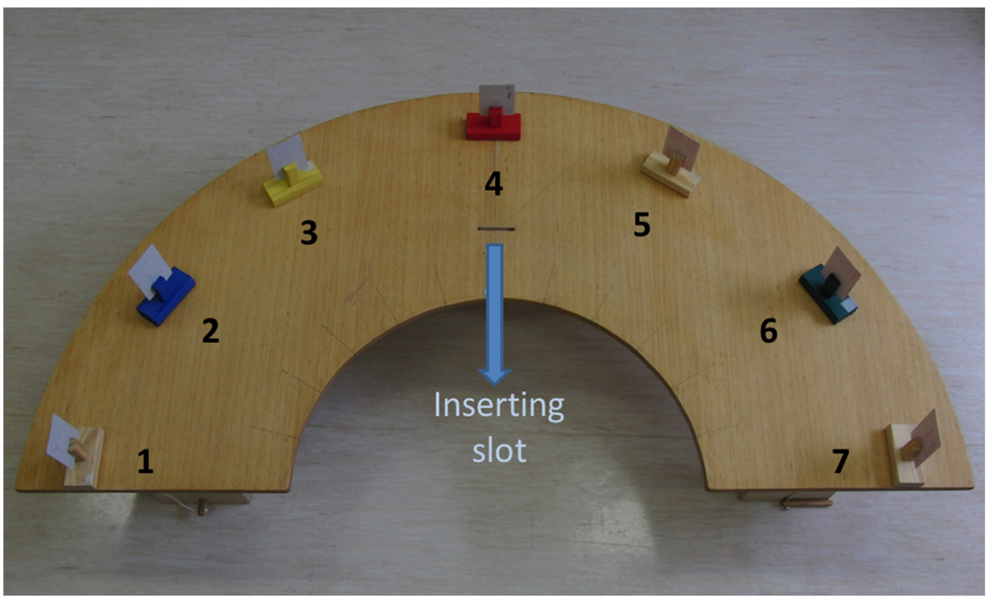

FIGURE 1 | Over-head perspective of the table surface showing the spatial arrangement of the cards (supported by holders) ranging from the leftmost (number 1) to the rightmost (number 7) position. Aligned with the position number 4 is indicated the slot used for inserting the cards in the complex task. Participants sat at the round opening of the table.

In the practice[2] phase, half the participants of each age group were assigned to an experimental or control group, with similar numbers of males and females in each group. During this phase, experimental groups practiced several reaching and manipulative tasks using their non-preferred left hand. Practice tasks consisted of (A) grasping wooden blocks scattered on a table and stacking them into small buildings; (B) employing index finger and thumb pinch-like movements, grasping small (1-cm diameter) balls in a container, transporting and inserting them into round openings on a board; (C) sequential sliding and turning upside down cards on a table; (D) tracking a small moving target on a computer screen through manipulation of a computer mouse; (E) sequential picking up of sticks scattered on a table, with the restriction of not moving the other sticks; and (F) moving bidirectionally 2-cm diameter round plastic pieces between left-right and proximal-distal positions aiming at spatial targets on a board (**Figure 2**). Practice tasks, thus, had some motor control requirements similar to those of the probing tasks, involving reaching and manipulation, but they were distinct in terms of movement specificity. Although the practice tasks required grasping, transporting and inserting skills, features like manipulated objects, range of motion across the workspace and movement amplitude were different between the practice and probing tasks. Those tasks were practiced with the participant sat at a table supporting the described task-related material. While the left hand was active in performing one task, the right hand was maintained motionless supported on the participant's lap. Participants practiced during 20 min per day twice a week, during 3 weeks, totalizing 120 min of practice in six sessions. In each session, four of the described tasks were practiced during 5 min each one. The six motor tasks were varied in a balanced way between sessions of practice, accumulating 20 min of practice for each one of the tasks at the end of this phase. Participants were instructed to perform the tasks at a self-paced rhythm, without emphasis on movement improvement across trials either in terms of accuracy or time. They were not provided with augmented feedback. Rest intervals of 30 s were introduced in the transition between sets of trials for each task. Experimental groups of both ages practiced the same tasks under experimenter's supervision. During the practice phase control groups had no activities associated with the experiment. Posttest was made 5 min after a passive rest interval following the last practice session, and retention was tested 20 days following posttest. In posttest and retention, procedures were the same as described for the pretest. Cameras acquisition frequency for recording of kinematic data was set at 240 Hz.

[2]We draw the reader's attention to our use of the term "practice" to mean a series of systematic motor activities to provide practical experiences without the purpose of motor learning, as this term usually implies.

DATA ANALYSIS

Manual preference was measured through the following equation: $(R - L)/(R + L)$, in which R represents number of trials performed with the right hand, and L represents number of trials performed with the left hand. This equation was applied separately for each card position by task, individually for each participant. The score varied between −1 and 1, in which negative values indicate prevalent use of the left hand, and positive values prevalent use of the right hand.

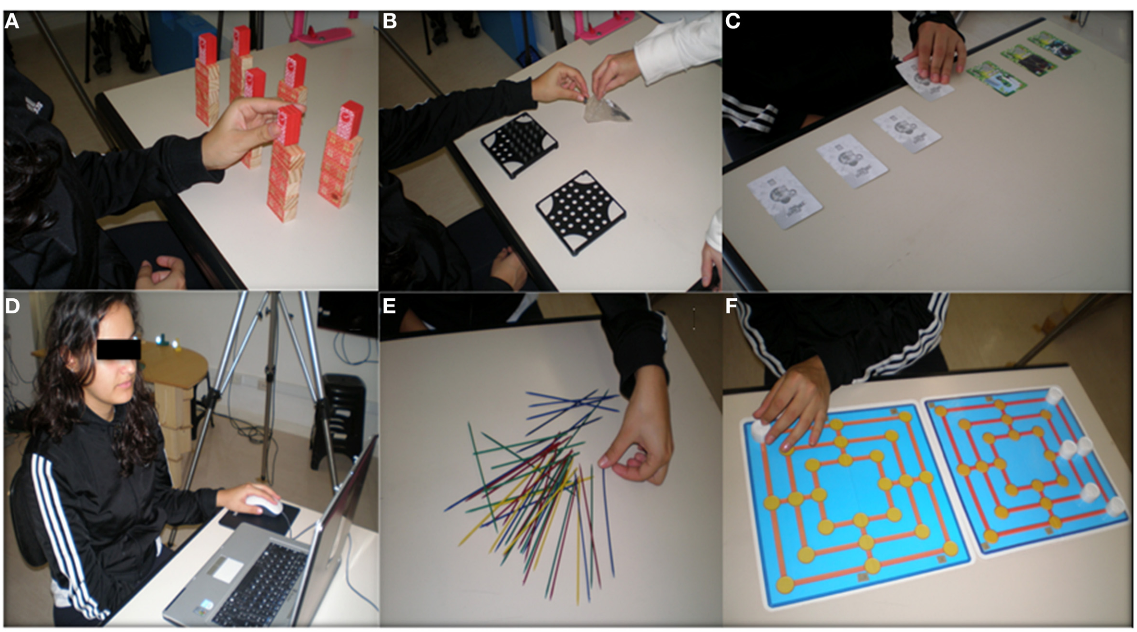

FIGURE 2 | Tasks used during practice. (A) stacking wooden blocks, **(B)** grasping and inserting small balls into openings on a board, **(C)** sequential upside down turning of cards on a table, **(D)** tracking a small moving target on the computer screen using a computer mouse, **(E)** sequential picking up of sticks, and **(F)** moving bi-directionally 2-cm diameter round plastic pieces between left-right and proximal-distal positions aiming at spatial targets on a board.

To assess motor performance, data were first digitalized through the Vicon Nexus software, and then data were analyzed through custom-made Matlab® (Mathworks, Inc., Natick, MA) routines. Prior to acquisition of kinematic data, participants performed three static trials keeping a block of six cards between the index finger and thumb. The average distance between finger markers was considered as the criterion to determine the moment at which the card was grasped at the end of reaching, and the time of fingers aperture to insert the card into the slot in the complex task. Movement analysis was divided into two components: reaching and transporting. Reaching initiation was defined as the moment that wrist velocity reached 5% of peak velocity, and its end was defined as the moment that between-finger distance achieved the criterion value. Initiation of the transporting component was defined as the moment of card grasping and its end at the time that the thumb was inside a virtual area delimited by a radius of 140 mm on the horizontal plane with its center at the middle of the slot, and the distance between the thumb's marker and a marker bordering the slot was equal to 70 mm in the *Z* coordinate. The following kinematic variables were evaluated for the reaching and transporting movement components: movement time; straightness score, given by the ratio of the distance between the initial wrist position and the card by hand displacement; number of movement units, given by the frequency of peaks sided by valleys in the velocity curve for which differences in instantaneous velocities were greater than 1 cm/s. Raw data was filtered through a dual-pass fourth order Butterworth filter with cutoff frequency set at 10 Hz.

RESULTS

MANUAL PREFERENCE

In order to have a perspective of the general effect of practice using the non-preferred left hand, in a preliminary analysis we pooled individual data of all target positions and task complexities to compare scores of manual preference across tests. **Figure 3** shows that descriptive analysis, suggesting a global trend toward reduced preference of the right hand in posttest and retention for both the adults and children experimental groups, whereas the respective controls showed a stable manual preference of their right hand. Decreased scores of manual preference following lateralized practice were due to the fact that at individual level most participants showed modulation of their hand preference. Analyzing enduring results of retention in comparison with the pretest, we observed the following: four participants maintained predominant use of their right hand but with decreased frequency, two shifted manual preference as indicated by predominant use of the left hand across target positions, whereas three participants showed no sensibility to left hand use during practice, maintaining the same manual preference between evaluations. These numbers were the same for each age group. For the statistical analysis presented in the following, we will describe significant effects only.

Statistical analysis of variation of scores of manual preference across tests was made separately for each card position by task complexity through Wilcoxon paired comparisons. Descriptive data from this analysis is shown in **Figure 4**. An overview of the several comparisons of task complexity by target position in that figure suggests that manual preference was affected by

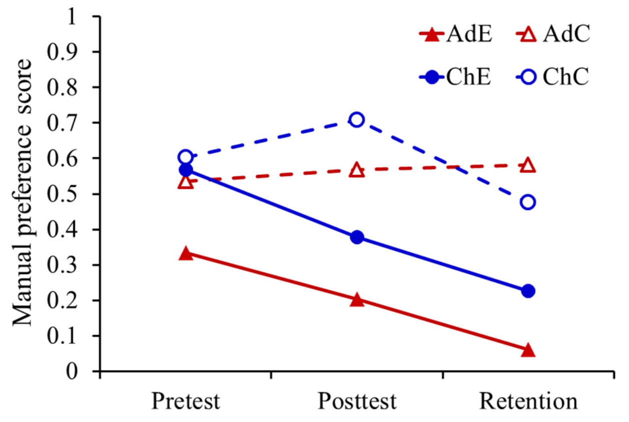

FIGURE 3 | Comparison of experimental and control age groups (Ad, adults; Ch, children; E, experimental; C, control), based on the global score of manual preference computed across all card positions, showing a trend of the experimental groups toward higher use of the left hand in posttest and retention as compared with pretest.

increased left hand use in most conditions for both the adults and children experimental groups. However, results showed significant effects of test for specific positions only, which were distinct between the experimental age groups. For the adults, significant differences were found on the simple task at the midline position: pretest × posttest ($Z = 1.99$, $p = 0.05$), and pretest × retention ($Z = 2.02$, $p = 0.04$). For the children, significant differences were found in the complex task: positions 6 and 7, pretest × posttest ($Z = 2.07$, $p = 0.04$, for both comparisons). Even though differences between pretest and retention did not reach statistical significance both for positions 6 ($p = 0.07$) and 7 ($p = 0.11$), no significant differences were found between posttest and retention comparisons (p-values > 0.58) for these positions.

MOVEMENT KINEMATICS

Representative curves of hand velocity (wrist marker) of the right and left hands are shown in **Figure 5**, comparing profiles between adults and children for the reaching (A) and transporting (B) components. Analysis of movement kinematics was made through a Four Way linear mixed model, 2 (group: control × experimental) × 2 (age: children × adults) × 3 (test: pretest × posttest × retention) × 2 (hand: right × left), ANOVAs with repeated measures on the last two factors. Analyses of kinematic variables of the components of reaching and transporting the card were made separately. **Table 1** presents descriptive kinematic data, comparing the right and left hands across tests. Results indicated absence of significant main effects or interactions associated with lateralized practice in the experimental groups in all analyses, as presented in the following.

REACHING FOR THE CARD

Analysis of movement time revealed significant main effects of group [$F_{(1, 34)} = 4.38$, $p = 0.04$], due to longer movement times in the control ($M = 1.06$ s, $SD = 0.24$) than in the experimental ($M = 0.99$ s, $SD = 0.21$) groups; age [$F_{(1, 34)} = 25.47$, $p = 0.001$], indicating that children ($M = 1.10$ s, $SD =$

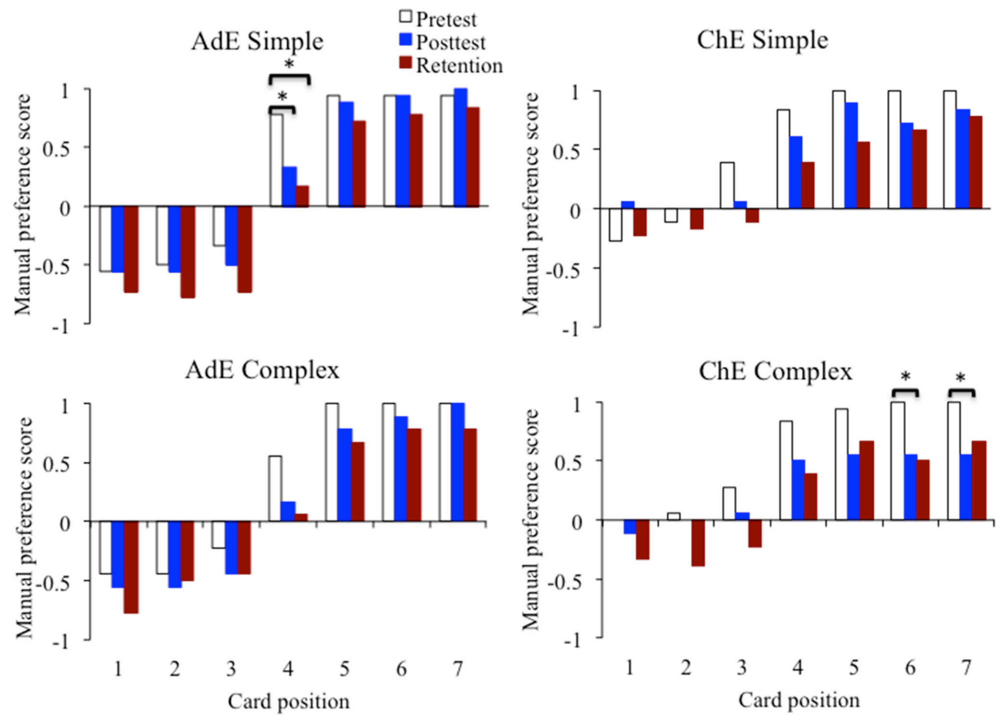

FIGURE 4 | Scores of manual preference for each card position, comparing values across tests (pretest, posttest, and retention). Left side panels show results for the adults and right side panels results for the children, upper panels show results for the simple and lower panels for the complex task. Statistically significant results are indicated by means of asterisks.

0.25) had longer movement times than adults ($M = 0.95$ s, $SD = 0.16$); and hand [$F_{(1, 34)} = 5.59$, $p = 0.02$], due to longer movement times of movements performed with the left ($M = 1.06$ s, $SD = 0.24$) than the right ($M = 0.99$ s, $SD = 0.20$) hand. Analysis of straightness revealed a significant main effect of age [$F_{(1, 34)} = 5.42$, $p = 0.02$], due to the fact that children ($M = 0.65$, $SD = 0.09$) presented lower values than adults ($M = 0.68$, $SD = 0.09$). Analysis of number of movement units revealed a significant main effect of age [$F_{(1, 34)} = 97.20$, $p = 0.001$], indicating that children ($M = 1.88$, $SD = 0.25$) presented an increased number of movement units than adults ($M = 1.04$, $SD = 0.84$).

TRANSPORTING THE CARD

Analysis of movement time revealed significant main effects of age [$F_{(1, 34)} = 63.44$, $p = 0.001$], indicating that children ($M = 1.61$ s, $SD = 0.40$) presented longer movement times than adults ($M = 1.26$ s, $SD = 0.29$); and hand [$F_{(1, 34)} = 41.00$, $p = 0.001$], due larger values for the left ($M = 1.57$ s, $SD = 0.41$) than for the right ($M = 1.29$ s, $SD = 0.31$) hand. Analysis of straightness revealed significant main effects of group [$F_{(1, 34)} = 7.38$, $p = 0.007$], indicating that controls ($M = 0.59$, $SD = 0.14$) presented higher values than the experimental ($M = 0.53$, $SD = 0.17$) groups; and hand [$F_{(1, 34)} = 9.74$, $p = 0.002$], due to higher values for movements performed with the right ($M = 0.59$, $SD = 0.16$) than with the left ($M = 0.53$, $SD = 0.15$) hand. Analysis of number of movement units revealed significant main effects of age [$F_{(1, 34)} = 79.10$, $p = 0.001$], indicating that children ($M = 2.84$, $SD = 1.47$) presented an increased number of movement units than adults ($M = 1.50$, $SD = 0.74$); and hand [$F_{(1, 34)} = 27.51$, $p = 0.001$], due to increased values for movements performed with the left ($M = 2.56$, $SD = 1.55$) than with the right ($M = 1.77$, $SD = 0.94$) hand.

DISCUSSION

The present experiment was designed to evaluate the effect of use of the non-preferred left hand in the practice of several tasks on manual preference to perform motor tasks different from those practiced. Evaluation was made in age groups acknowledged to have consistent manual preference, comparing tasks and spatial arrangements inducing distinct frequencies of right/left hand use. At a descriptive level, analysis showed an overall trend toward increased preference of the left hand following practice, with some cases of shift to global left hand preference in both age groups. Statistical analysis indicated that the effect of left hand practice on manual preference reached significance at specific tasks/positions. For the adults, increased preference for the left hand was observed at the midline position for the simple task, while for the children use of the left hand during practice modulated manual preference in the two rightmost target positions in the complex task. The observed effects were persistent over 20 days of rest, and were not associated with variation of intermanual performance asymmetry. Results are in agreement with the expected diffusion of manual preference acquired through systematic hand use over manual preference of distinct motor tasks.

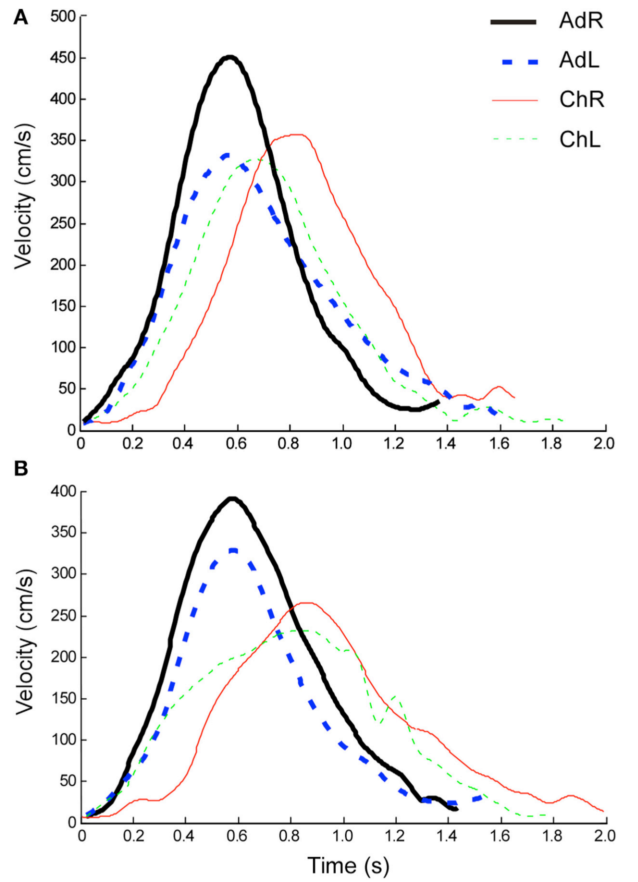

FIGURE 5 | Representative hand velocity (cm/s) curves of single trials for the reaching (A) and transporting (B) components of the task, comparing hand profiles between age groups. Ad, adults; Ch, children; R, right; L, left.

A preliminary point to consider in the results is that power of modulation of manual preference by left hand practice was less evident than has been found in previous investigation in children (Teixeira et al., 2010) and adults (Teixeira and Okazaki, 2007), with significant effects only at specific probing conditions for each age group. Limited modulation of manual preference in the present results might be thought to derive from different points. First, even though we used reaching and manipulative tasks during practice, just a few of those tasks were strictly similar to the tasks employed to probe manual preference. As we showed in previous results, diffusion of manual preference between tasks was stronger when the probing task was similar in its sequential structure to that practiced (Teixeira and Okazaki, 2007). For another probing task requiring a different sequential structure the diffusion of manual preference was less evident. From these results, it seems that similarity between practice and probing tasks is a factor limiting the diffusion of manual preference resulting from lateralized practice. Second, we tested age groups expected to be consistent in the use of the right hand, a feature particularly evident in the children at the age employed in this experiment (cf. Bryden and Roy, 2006; Doyen et al., 2008; Hill and Khanem, 2009). This aspect may have attenuated a more generalized effect of left hand practice on manual preference as has been previously found in young children (Teixeira et al., 2010). It is plausible that, as young children are inconsistent in manual preference (Gesell and Ames, 1947; Carlier et al., 2006; Leconte and Fagard, 2006; Doyen et al., 2008; Hill and Khanem, 2009; Bryden et al., 2011), they are more strongly affected by using a single hand. By considering the lack of task specificity and that we tested groups of consistent manual preference, on the other hand, results of persistent modulation of manual preference by systematic use of the left hand indicates the power of lateralized experiences in the development of a generalizing bias in hand selection for motor performance. Some noticeable cases were those in which manual preference in the probing tasks was shifted toward the left hand, as indicated by the global score across card positions, in both age groups. This result suggests that consistent use of the left hand to perform motor tasks can induce not only a more frequent use of that hand but also its prevalent use over the globally preferred right hand. Further on this point, we highlight the finding that such a persistent modulation of manual preference over several days of rest was achieved from a moderate amount of practice regarding the number of motor experiences accumulated with the preferred right hand in daily living activities. These findings support the notion that manual preference is a dynamic component of motor behavior continuously open to change.

Left hand practice induced modulation of manual preference differently between children and adults. For the adults the most noticeable change of manual preference following practice took place at the midline. Although the effect of practice was significant for the simple task only, the same trend was observed also for the complex task. This result is consistent with a previous finding showing that increased use of the non-preferred hand as a result of feedback manipulation in adults is more evident at the central in comparison with lateral positions (Stoloff et al., 2011). We interpret this result in the light of previous findings suggesting that there is a competition between motor plans to perform an action with either the right or the left hand (Oliveira et al., 2010). In situations in which the target is located at a lateral position in the workspace, proximity between the hand and the target (Gabbard and Helbig, 2004; Helbig and Gabbard, 2004) and biomechanical constraints (Carey et al., 1996; Bryden and Huszczynski, 2011; Kim et al., 2011) introduce a contextual transient bias in hand selection. At the midline position, however, there is no physical advantage for either hand. Then, at this position higher frequency of use of a single hand can be thought to express more clearly a relatively permanent global bias of hand selection. From the comparison between age groups, it becomes apparent that adults attribute a larger weight to contextual biomechanical constraints than to the global bias in hand selection as compared to children. This conclusion is consistent with the finding that adults privilege a comfort state in hand selection in detriment of the global lateral bias (cf. Coelho et al., 2014). For the children, increased manual left hand preference at the two rightmost target positions after practice is consistent with previous findings in younger children showing a more evident modulation of manual preference due to left hand practice in targets positioned in the right hemispace (Teixeira et al.,

Table 1 | Comparison of kinematic landmarks between the left and right hands across tests.

	Reaching						Transporting					
	Left			Right			Left			Right		
	Pretest	Posttest	Retention	Pretest	Posttest	Retention	Pretest	Posttest	Retention	Pretest	Posttest	Retention
EXPERIMENTAL ADULTS												
Movement time (s)	0.93 (0.16)	0.95 (0.12)	0.92 (0.15)	0.89 (0.15)	0.92 (0.12)	0.88 (0.14)	1.34 (0.27)	1.40 (0.22)	1.21 (0.23)	1.09 (0.17)	1.10 (0.18)	1.06 (0.23)
Straightness score	0.71 (0.08)	0.73 (0.06)	0.68 (0.10)	0.66 (0.10)	0.71 (0.80)	0.68 (0.08)	0.51 (0.15)	0.50 (0.16)	0.51 (0.21)	0.59 (0.18)	0.58 (0.19)	0.63 (0.14)
Movement units (*n*)	1.08 (0.13)	1.03 (0.08)	1.03 (0.08)	1.11 (0.22)	1.03 (0.08)	1.03 (0.08)	2.04 (0.78)	1.77 (0.47)	1.48 (0.31)	1.39 (0.64)	1.35 (0.51)	1.22 (0.34)
CONTROL ADULTS												
Movement time (s)	1.00 (0.13)	1.04 (0.18)	0.98 (0.15)	1.04 (0.22)	0.94 (0.18)	0.96 (0.20)	1.41 (0.21)	1.55 (0.34)	1.39 (0.39)	1.16 (0.29)	1.14 (0.29)	1.24 (0.19)
Straightness score	0.65 (0.11)	0.69 (0.10)	0.65 (0.08)	0.73 (0.10)	0.69 (0.10)	0.67 (0.08)	0.57 (0.15)	0.58 (0.15)	0.57 (0.13)	0.60 (0.19)	0.62 (0.18)	0.63 (0.16)
Movement units (*n*)	1.15 (0.14)	1.13 (0.33)	1.06 (0.11)	1.29 (0.38)	1.06 (0.11)	1.00 (0.00)	1.97 (0.85)	2.13 (1.06)	1.61 (0.44)	1.25 (0.33)	1.55 (0.47)	1.53 (0.52)
EXPERIMENTAL CHILDREN												
Movement time (s)	1.12 (0.23)	1.12 (0.21)	1.14 (0.26)	1.06 (0.19)	1.06 (0.24)	0.97 (0.30)	1.71 (0.36)	1.80 (0.45)	1.91 (0.46)	1.39 (0.33)	1.38 (0.29)	1.49 (0.36)
Straightness score	0.64 (0.07)	0.67 (0.07)	0.68 (0.12)	0.68 (0.07)	0.67 (0.10)	0.59 (0.05)	0.44 (0.18)	0.44 (0.15)	0.52 (0.19)	0.54 (0.17)	0.58 (0.14)	0.53 (0.17)
Movement units (*n*)	1.83 (0.75)	1.96 (0.79)	2.89 (0.74)	1.69 (1.19)	1.61 (0.58)	1.60 (0.63)	3.58 (1.49)	3.42 (1.57)	3.58 (1.32)	2.34 (0.96)	2.60 (0.96)	2.07 (0.63)
CONTROL CHILDREN												
Movement time (s)	1.15 (0.27)	1.31 (0.44)	1.10 (0.21)	1.04 (0.20)	1.04 (0.20)	1.11 (0.24)	1.73 (0.41)	1.59 (0.45)	1.84 (0.43)	1.43 (0.22)	1.60 (0.39)	1.42 (0.28)
Straightness score	0.64 (0.10)	0.67 (0.15)	0.70 (0.05)	0.65 (0.08)	0.65 (0.06)	0.62 (0.10)	0.61 (0.09)	0.55 (0.13)	0.52 (0.13)	0.67 (0.11)	0.56 (0.16)	0.59 (0.12)
Movement units (*n*)	1.68 (0.77)	1.70 (0.59)	1.62 (0.71)	1.30 (0.23)	1.31 (0.57)	1.45 (0.71)	3.22 (1.43)	2.54 (1.21)	4.07 (2.68)	2.29 (1.07)	2.62 (0.95)	2.36 (0.82)

Average values with standard deviation shown in parenthesis, separately for the reaching and transporting components.

2010). However, even though increased preference of the left hand after practice was found to be significant at the two rightmost positions only, a similar trend can be observed for the other right sided positions. This result seems to reflect a particular characteristic of modulation of manual preference by use in the children. For target positions in the right hemispace there are two physical factors biasing selection of the right hand, namely target proximity (Gabbard and Helbig, 2004; Helbig and Gabbard, 2004) and mechanical efficiency (Carey et al., 1996; Bryden and Huszczynski, 2011; Kim et al., 2011). Combination of these two contextual factors with a global bias to select the preferred right hand seems to be responsible for an almost exclusive use of that hand to reach for and manipulate right-sided targets before practice, which is in consonance with previous findings (cf. Bryden and Roy, 2006; Carlier et al., 2006; Doyen et al., 2008; Hill and Khanem, 2009). The fact that the children increased frequency of use of the left hand in right-sided positions following practice suggests that the global lateral bias toward using the left hand was strong enough to overcome the contextual spatial-related bias of those target positions inducing selection of the right hand. The finding that use-dependent modulation of manual preference took place in the complex task in the children suggests that they became highly confident in using their left hand even when the task required increased manipulation accuracy. This finding is contradictory with the supposition that the non-preferred hand is more probably used in tasks requiring simple movements. It becomes apparent that following practice the children became confident in using their left hand to perform tasks requiring crossing the midline and demanding increased accuracy. This characteristic sharply contrasts with the pretest results, in which not a single case was observed of reaching for the rightmost card positions with the left hand. Hence, an important point emerging from our results is that children at this age, although reported to be highly consistent in the selection of their right hand (e.g., Bryden and Roy, 2006), were shown to be malleable to the effect of hand use. From this finding, it might be thought that some environmental factor taking place regularly in daily living experiences at this age, like increased unimanual use for handwriting, leads to high consistency in the preference of the right hand to perform several other motor tasks.

A point to be underscored in the results was that increased use of the left hand following practice was not paralleled by a change of intermanual performance asymmetry in movement kinematics. Absence of change in the between-hand relationship of motor performance following left hand practice was foreseen at the experiment outset, since the practiced motor tasks were distinct from those used to evaluate manual preference and there was no emphasis on improvement of motor performance during practice. Modulation of manual preference by means of left hand practice, then, was shown to vary as a consequence of lateralized use rather than to development of manual asymmetry favoring the left hand. From this result, it is implausible that modulation of manual preference have been a consequence of an improved capacity to perform the probing tasks with the left hand, or due to less attentional effort due to movement automatization. This is an important point for a theory of lateralization of motor behavior, since prevalent models of human laterality are based on the assumption that manual preference derives from cerebral hemisphere dominance and associated intermanual performance asymmetry (Annett, 1972; Levy and Nagylaki, 1972; McManus, 1985). Przybyla et al. (2013) have presented evidence suggesting that relative better performance of the non-dominant left hand in aiming movements performed in the absence of visual feedback biases manual preference for that hand. However, it should be considered the possibility that higher frequency of use of the left hand in Przybyla's results may have been due not to performance improvement *per se*, but to the sense of higher likelihood of success when using the non-dominant left hand. This interpretation is based on Stoloff et al. (2011) findings that perception of greater proficiency of the non-preferred hand, without effective improvement of movement control, leads to higher probability of its use to perform a motor task. Stoloff's results suggest that hand selection in a given trial is biased by confidence of success when using a given hand, established from the history of previous experiences. In line with this rationale, we interpret our results from the perspective that use of the non-preferred left hand in different manual tasks increased the confidence on that hand to perform movements requiring accuracy. The finding that the practiced tasks were not specific for the evaluation of manual preference suggests that increased confidence on one hand diffuses over distinct motor tasks, inducing a global bias in hand selection. We propose that increased confidence on the capacity to control proficiently movements of a given hand leads to a predisposition to plan movements for that hand, even in cases that a task is performed for the very first time. We conceptualize confidence on hand performance as a high-level component of movement organization affecting decision making about hand selection in a variety of motor tasks, which we name as "diffusion." Convergent to this proposition, Sabaté et al. (2004) have shown that in tasks requiring rapid finger movements, different movement times between hands in physical execution are expressed also in movement imagery. Sabaté has proposed that the brain scans the motor competence of the limbs, adjusting the planning of future movements to their estimated capability. This level of movement organization, then, is able to have a pervasive effect on manual preference. From this notion, it is possible that the expected poor performance with the non-preferred hand in daily living situations leads to planning movements for the preferred hand, leading to a higher frequency of its use.

As concluding remarks, we underscore the finding that modulation of manual preference following left hand practice was shown to be due to left hand use *per se* rather than to improvement of proficiency in the performance with the left hand. This finding indicates that manual preference is not fundamentally associated with intermanual performance asymmetry. However, as manual skill rapidly improves at the beginning of lateralized practice, consistent selection of a single hand to perform a task is expected to lead to intermanual performance asymmetry favoring either the right or the left hand (cf. Teixeira, 1999, 2000), reinforcing the confidence on the selected hand for motor performance. The finding that modulation of manual preference was achieved through practice of non-specific motor tasks supports the conceptualization of diffusion of manual preference from the practiced over different movements. Although children and adults were affected in particular ways by left hand practice, both age groups showed malleability to modulate manual preference as a result of the recent history of differential use between the hands. As these age groups are acknowledged to have consistent manual preference for the right hand, we consider to have made a strict test of the effect of hand use on manual preference in this experiment. Our results, then, offer an alternative interpretation for lateralization of behavior, which may be based on systematic single hand use in a set motor tasks and diffusion of the resultant manual preference over several distinct motor actions.

ACKNOWLEDGMENTS

Rosana M. Souza was supported through a studentship provided by the Foundation for Research Support of the State of São Paulo (FAPESP #2010/01581-9), and Luis A. Teixeira was financially supported through grants provided by the Brazilian Council of Science and Technology (CNPq #303052/2010-4), and CAPES, Brazil.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 30 September 2014; accepted: 17 November 2014; published online: 04 December 2014.

*Citation: Souza RM, Coelho DB and Teixeira LA (2014) Modulation of manual preference induced by lateralized practice diffuses over distinct motor tasks: age-related effects. Front. Psychol. **5**:1406. doi: 10.3389/fpsyg.2014.01406*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 15 January 2015
doi: 10.3389/fpsyg.2014.01585

Age and practice effects on inter-manual performance asymmetry

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Manual dexterity declines with increasing age, however, the way in which inter-manual asymmetry responds to aging is unclear. Our purpose was to determine the effect of age and practice on inter-manual performance asymmetry in an isometric force pinch line tracing task that varied in difficulty within segments. Thirty right-handed participants, five males and five females in each of three age groups, young (Y20), young–old (O70), and old–old (O80), practiced an isometric force pinch task for 10 trials with each hand on each of five consecutive days. Inter-manual performance asymmetry of the right and left hands was analyzed with a repeated measures analysis of variance (ANOVA) of asymmetry with age groups, practice, task difficulty, and hand as factors. The within-individual magnitude of asymmetry was also analyzed with a repeated measures ANOVA of manual asymmetry calculated as an asymmetry index (AI). *Post hoc* pair-wise comparisons were performed when significance was found. We observed no inter-manual performance asymmetry on this isometric tracing task among any of the age groups, either in the hand performance differences or in the magnitude of the AI. Age and practice interacted in terms of manual performance: the Y20 and O70 group improved *accuracy and task time* across the 5 days of practice but the O80 group did not. However, practice did not differentially affect the AI for *accuracy or task time* for any group. Accuracy of performance of the two hands was differentially affected by practice. All age groups exhibited poorer performance and larger AIs on the most difficult segments of the task (3 and 6) and this did not change with practice.

Keywords: manual asymmetry, force control, aging, inter-manual performance asymmetry, HAROLD

INTRODUCTION

Inter-manual asymmetry, the commonly observed phenomenon that most humans use their right hand to execute high precision motor tasks, has been reported to develop throughout childhood and peak when young and middle-aged adults reach their highest level of skill (Raw et al., 2012; Gooderham and Bryden, 2013). Manual dexterity of both hands deteriorates with aging due to changes in neuromuscular structure and function as well as age-related declines in hand use and general physical activity (Carmeli et al., 2003; Ward and Frackowiak, 2003; Kalisch et al., 2006). Teixeira (2008) categorized manual tasks into three profiles: those associated with an asymmetrical right hand advantage (handwriting, aiming throwing, and maximal grip strength); more symmetrically performed tasks (anticipatory timing, grasping moving objects, and twisting and drilling performance); and tasks associated with asymmetrical left hand advantage (hand posture tasks). However, the effects of aging on inter-manual performance asymmetry has not been resolved, although most agree that age effects on inter-manual performance asymmetry are task-specific (Provins, 1997; Seidler, 2007; Teixeira and Teixeira, 2007; Raw et al., 2012; Saucedo Marquez et al., 2013).

Some studies found that older adults demonstrate less manual asymmetry than young adults, especially on tasks that have been observed to be highly lateralized (Teixeira, 2008). Examples are button pressing (Mattay et al., 2002; Rowe et al., 2006) manually tracing lines (Raw et al., 2012) and reaching tasks (Przybyla et al., 2011). Two models have been proposed to explain hemispheric asymmetry changes with age: the hemispheric asymmetry reduction in older adults model (HAROLD; Cabeza, 2002) and the right hemisphere aging model (Dolcos et al., 2002). According to the HAROLD model, prefrontal cortex activity tends to be less lateralized in older adults when compared to young adults as seen in cognitive tasks where older adults tend to show more bilateral activations than young adults (Cabeza, 2002). Przybyla et al. (2011) applied the HAROLD model to motor performance and found a reduction in manual asymmetries in older adults performing a horizontal plane reaching task. The right hemisphere aging model suggests that age-related cognitive declines affect functions located in the right hemisphere more than functions located in the left hemisphere (Dolcos et al., 2002). Weller and Latimer-Sayer (1985) found support for this model using a simpler task, the peg-board task, where older adults showed greater decline in left hand performance (hence right cortex function) than in right hand performance.

In addition to comparing performance between the right and left hand, researchers have measured inter-manual performance asymmetry by calculating the *differences* between the hands; that is, the extent of asymmetry within each person which can be measured as a within-person score or asymmetry index (AI) metric. A few investigators, using AI as a measure of the magnitude of difference between participants' two hands' performances, have found that older adults are more asymmetrical when compared to young adults on certain tasks, such as grasp control (Chua et al., 1995), graphic tracing (Francis and Spirduso, 2000), and graphic drawing (Teixeira, 2008). However, Teixeira (2008) also reported that these same older adults were less asymmetrical than younger adults when hand grip strength was assessed. Therefore, more research is needed to clarify age effects on inter-manual performance asymmetry.

Several researchers have analyzed the effects of practice on manual asymmetry. Asymmetries observed in young adults on movement tasks have been shown to be dramatically changed with task-specific practice (Peters, 1976; Perelle et al., 1981; Bryden and Allard, 1998; Teixeira and Teixeira, 2007) and these changes even generalized to a different but similar motor task (Teixeira and Okazaki, 2007). In several studies of young adults performing movement tasks, the non-preferred hand benefitted more from practice and thus inter-manual performance asymmetry was decreased in highly lateralized tasks such as drawing shapes (Halsband, 1992) and reverse printing (Parlow and Kinsbourne, 1989). Conversely, Perelle et al. (1981), who provided 5 days of practice on a manipulative dexterity test, found that both hands improved similarly. Practice has been shown to reveal age-related reductions in inter-manual performance asymmetry in transfer of training studies, in which benefits derived from practice of one limb were not equally transferred to the other limb. Inter-limb transfer of trajectory direction information for a reaching task occurred only from the non-dominant to the dominant arm for young adults, whereas final position information transferred in both directions in older adults (Wang et al., 2011; Pan and Van Gemmert, 2013).

The characteristics, profiles, and proposed mechanisms of inter-manual performance asymmetry in young and old adults, discussed above, have focused on coordinated movement tasks that require not only central planning and execution but also substantial information processing of neuromuscular-generated feedback during the movement. Relatively few studies of the effects of aging on possible inter-manual performance asymmetry of dynamic force control have been conducted, and even fewer are available regarding the effect of age and practice on these asymmetries. Two studies, both using isometric force control to move a computer cursor to screen targets, have shown that differences between young and old can be reduced to non-significance with practice. Christou et al. (2007) reported that after just 35 trials of practice with the left (non-preferred) hand, no age differences remained groups on endpoint force accuracy, although the age groups still differed in the adjustments made in motor-output variability and muscle activity associated with the initial improvements. Poston et al. (2008), also found that the left hand of older adults exhibited greater errors than those of young on the first day of practice, but these differences were eliminated by two additional days of practice, whether the practice was with the right or the left hand. Conversely, several other investigators, providing multiple trials over more than 1 day showed that older adults improved dynamic isometric force control tracing and tracking when they performed and practiced with one hand, but not as much as young adults improved (Spirduso and Choi, 1993; Lazarus and Haynes, 1997; Voelcker-Rehage and Alberts, 2005; Francis et al., 2012). Lazarus and Haynes (1997) found no age differences in the transfer of information from one hand to the other in a transfer of training paradigm requiring participants to track isometrically a randomly generated template. For all age groups, whichever hand practiced second made fewer errors, benefitting from the previously practiced contralateral hand.

In this study we examined the interaction of age and practice on inter-manual performance asymmetry of unilateral isometric force control for each hand, particularly with regard to whether older adults are less asymmetrical than young adults, and whether the magnitude of inter-manual performance AI is lower in older adults. We also examined the interaction of age and practice, to determine what effect 5 days of practice has on inter-manual performance asymmetry and AI. Finally, because it is well-documented that age differences in motor task performance increases as task difficulty increases (Voelcker-Rehage, 2008), we used a force control template shown to have two segments requiring greater control than the other four, to determine whether inter-manual asymmetries and AI are influenced by age and practice and task difficulty.

MATERIALS AND METHODS

PARTICIPANTS

Thirty participants, five males and five females in each of three age groups: Y2 (mean age = 21.4 years, SD = 3.6, age range: 18–23 years), O70 (mean age = 69.7 years, SD = 2.6, age range: 65–74), and O80 (mean age = 78.5 years, SD = 2.8, age range: 75–84). The age range for the two older age groups were chosen because 65–74 is often referred to as the "young–old" while the 75–84 is termed the "old–old" (Spirduso et al., 2005b). The young adults were undergraduate volunteers from a university. The older adults were recruited from the local community and all had completed some college (mean years of school = 16.2 years, SD = 2.6). All participants were right-handed according to the Edinburgh handedness inventory (minimum score for right hand dominance = +0.90; Oldfield, 1971), with normal to corrected vision, no diagnosed cognitive or neurological disorders, free of severe arthritis, could ambulate unassisted, and lived independently with no prior experience with the apparatus. Participants gave informed consent (approved by two university IRB boards) affirming their willingness to participate in this research study.

INSTRUMENTATION

The manual force quantification system (MFQS) was designed to quantify low levels of isometric force control in a dynamic pinch task that requires modulation of inter-digit forces (Spirduso et al., 2005a). The instrumentation quantified the amount of force applied to each of a pair of transducers by individual digits, either the thumb or index finger of the (preferred) right hand or those of the (non-preferred) left hand. The amount of force produced by each digit was manifested directly as the position of a cursor on a computer screen such that one force transducer controlled the cursor movement parallel to a horizontal x-axis, and a second force transducer controlled the cursor movement parallel to a vertical y-axis.

A 45° tracing template, representing equal forces from each digit, was projected onto a monitor screen and included the target line connected by *Start, Reverse,* and *End* circles (**Figure 1**). Tracing in this task required the participant to begin and end the task at circles located respectively at the identical position on the computer screen. The participant had a full view of the current position of the cursor, but was provided no displayed retention of the cursor's cumulative tracing trajectory. The first part of the task required a net force application to move the cursor from the *Start* to the *Reverse* circle. The second part of the task required a net decrease in force from the *Reverse* to the *End* circle. Each of the circles lit up and a beep was heard when the cursor first contacted its own radius of acceptance, 0.098 newtons (N) in each instance.

The MFQS apparatus was comprised of two strain gages mounted to a base on a platform that was positioned and locked into place for each participant. The heel of the hand was anchored on the console and remained in contact with the console throughout the trial. The range of each strain gage was 0 to 4.45 N and the non-linearity of each was less than 1%. Force from the thumb controlled the cursor position on the horizontal x-axis and force from the index finger controlled the position on the vertical y-axis. Thus, simultaneous force of equal magnitude exerted by both digits kept the cursor on the 45° tracing line template with perfect geometric accuracy. This instrumentation also allowed for independent isometric force measurements by either digit. In this study, because the highest level of force required by the task at the return circle was only 7 N (simultaneous application of 3.5 N with the thumb and 3.5 N with the index finger), neither strength nor fatigue was a confounding factor. According to Herring-Marler et al. (2014) the average maximum pinch strength (combined thumb and finger forces) for older adult women and men was ~49 and 71 N respectively. Therefore the upper boundary of the high, middle, and low force levels of this task were 11, 8.4, and 5.8% of their mean maxima.

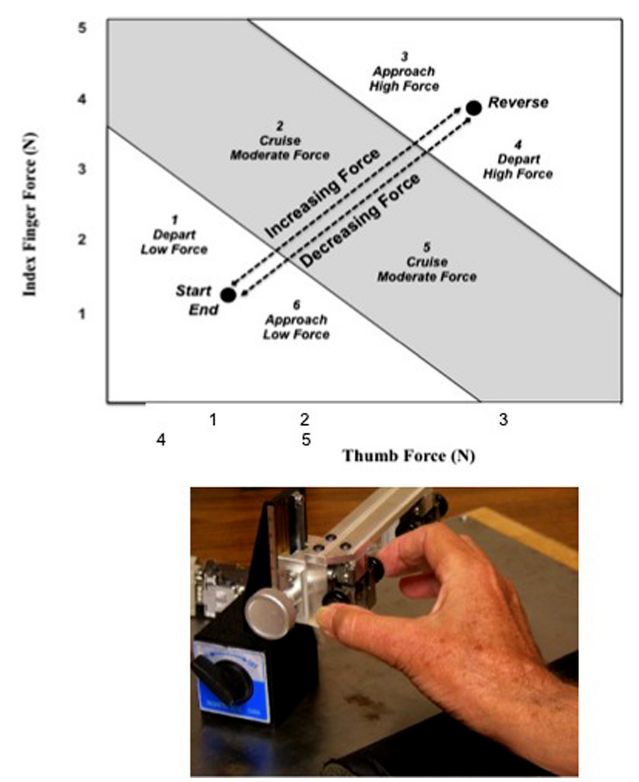

FIGURE 1 | Force tracing template parsed by segment categories. The lower black filled circles indicate both the *Start* and *End* circles and the upper black filled circle indicates the *Reverse* circle. The *Start* circle is associated with Segment 1 (depart, increasing force); the *Reverse* circle is associated with both Segment 3 (approach, increasing force) and Segment 4 (depart, decreasing force); and the *End* circle is associated with Segment 6 (approach, decreasing force). Segment 2 (cruise, increasing force) and Segment 5 (cruise, decreasing force) are not associated with circles. The segment locations and numbers are not visible to the participant, but are developed post-data collection for statistical analyses.

At each sampling instant (200 Hz) the instrumentation automatically recorded the thumb and finger force values along with a numerical value assigned to those data pairs which identified the current force level of the task in terms of increasing or decreasing force modulation. The software provided continuous timed data collection during the course of a trial and a visual display showing the cursor position to the participants. The data acquisition for this experiment utilized a virtual instrument (VI) application constructed with LabVIEW (National Instruments). Raw data for each trial were collected as a time series of horizontal and vertical cursor coordinate positions. Values were converted from grams to the corresponding force amplitude values in newtons (N). Trials that revealed a lapse or discontinuity in performance, such as intermittent gaps in which the release of contact with one or both strain gages was apparent, were discarded.

The target line was spatially divided into six equal task segments as shown in **Figure 1**. The segments were categorized by their proximity to a target: *Start*, *Reverse*, and *End* circles. The segments could also be distinguished by force level: low (5.8%), middle (8.4%), and high (11.0%). Thus each segment can be defined as follows: (1) *departing Start* circle, increasing force, low force level; (2) *cruising*, increasing force, middle force level; (3) *approaching* Reversal circle, increasing force, high force level; (4) *departing* Reversal circle, decreasing force, high force level; (5) *cruising*, decreasing force, middle force; and (6) *approaching End* circle, decreasing force, low force. The segmentation was created *post hoc* during the analysis and participants had no knowledge or visual indication of these categories. These segments were a factor that was included in the analysis, but they were not visible and were thus unknown to the participants. Our previous research has consistently shown that more errors are made and more time taken to approach the target or to reverse force direction (Spirduso et al., 2005b; Griffin et al., 2009; Eakin et al., 2012; Francis et al., 2012; Herring-Marler et al., 2014).

PROCEDURES

After giving consent, the participant was seated directly in front of the computer monitor, with the index finger and thumb of the right or left hand (hand order counterbalanced) resting on the console transducers and the arm bent at the elbow, forearm in a sagittal plane. To enhance consistency of performance and eliminate any confounding by wrist flexion, the participant kept the ulnar border of the hand anchored on the console box at all times. The thumb was positioned on the transducer nearest the participant and the index finger was positioned on the other strain gage button. Fingers not being used for contact with the strain gages were kept in a static and comfortably flexed position with no force exertion against any surface. The goal of the task was to coordinate the forces between the thumb and index finger by increasing or decreasing pressure to the transducers in such a way that the cursor progressed along the target line on the computer monitor from one circle to another (**Figure 1**).

Each participant completed an initial screening test that involved joystick control, before beginning the MFQS trials. The screening test used the same tracing template as the MFQS task except that the cursor was manipulated by single-hand positioning of a joystick which controlled the cursor on both x and y axes simultaneously. This screening task was intuitive and was easily accomplished by all participants, but because the testing set-up, task goals, and templates were exactly the same as in the force control task, it provided an efficient assessment of the participants' basic comprehension of the force control task instructions and instilled confidence in his/her ability to execute the task. This screening task also provided an indication of whether visual-spatial problems existed that would confound the assessment of force control.

Participants were tested five consecutive days and each testing session lasted ∼1 h. Each of the 5 days of practice followed the same protocol, except for the first day, which included signing the consent form, listening to the instructions, and performing two joystick trials with the right and left hands. This was followed by two practice trials with the right and left hands on the tracing task, and then 10 MFQS tracing trials for each hand. Hand order was counterbalanced across days. On each of the following 4 days, 10 trials were completed for the right and left hands. Participants were instructed "to complete the task as fast and accurately as possible." Accuracy was based on the ability to maintain contact with the tracing line throughout the tracing.

STATISTICAL ANALYSES

In order to examine inter-manual asymmetry between-hands and within-person and we conducted two repeated measures analysis of variances (ANOVAs). The first analysis was a mixed model ANOVA designed to determine if there were performance differences between the right and left hand that were related to the independent variables of Age (Y20, O70, O80), Days (1–5), and Segments (1–6) for Time and root mean square error (RMSE). *Post hoc* pair-wise comparisons were performed when significant results were found. The dependent measures for this analysis were the (1) natural logarithm of time in seconds required to traverse the entire task from *Start* circle to *End* circle and (2) accuracy, inferred from directly measured RMSE. The RMSE of an individual trial was determined by the collective individual error magnitudes from each sampling instance. That individual sampling error was the shortest distance (perpendicular line) from the cursor position to the template line because the error could not be allocated separately to the two digits if the target were a line rather than a single position.

Thus the individual error for a particular sampling i was

$$e_i = \frac{x_i - y_i}{\sqrt{2}}$$

and RMSE was defined as

$$RMSE = \sqrt{\frac{\sum_{i=1}^{N} e_i^2}{N}}$$

This indirect measure of accuracy represents the deviation from a perfect performance which would require a participant to increase and decrease force equally between the thumb and index finger, thus moving the cursor directly on the line between circles. The greater the distance between forces contributed by each digit at any sampling instance, the higher will be the contribution to the RMSE score and the less accurate will be the performance relative to the goal of the task.

A second ANOVA was performed on the absolute AI, in which the between-group factor was Age and the repeated measures were Days (1–5) and Segment (1–6). This analysis was designed to determine if there were significant differences in the magnitude of within-person manual asymmetry for Time and RMSE. *Post hoc* pair-wise comparisons were performed when significant results were found. The dependent measures for this analysis were the absolute AI for Time and RMSE. An AI was derived for each segment of each paired right and left hand trial sequence position on each practice day for each participant, based on the method of Teixeira and Teixeira (2007). The pairings were temporal such that the first right hand trial of a particular day was paired with the first left hand trial of that day, and so forth. If R_{ij} represents a variable score for segment j of right hand trial i and L_{ij} represents the score for segment j of the paired left hand trial, then the asymmetry magnitude for the paired segment was

$$A_{ij} = \left| \frac{R_{ij} - L_{ij}}{R_{ij} + L_{ij}} \right|$$

and the AI dependent variable for segment j, reflecting A_{ij} values for that segment over N trial pairs, was

$$AI_j = \sum_{i=1}^{N} \frac{A_{ij}}{N}$$

where, $N = 10$ for sets with no discarded performances. Pair-wise comparisons were performed when further *post hoc* analyses were indicated.

The data for 30 participants were initially organized by trial for a total of 3000 trials, or 20 trials (10 for the right and 10 for the left hand) on each of 5 days. Six scores for each dependent variable were produced for each trial because the task contained six segments. Trials that did not meet the pre-established criteria were removed from further analysis. Because the missing trials were few (<1% of data) and scattered among participants, testing for bias was unnecessary. The Estimation–Maximization technique was used to replace missing values using the mean for participant's trials on a given day. The time scores did not meet the criteria for assumption of a normal distribution. However, the natural logarithms of the time scores did meet such criteria, so that transformed time scores were used for statistical significance evaluations. To keep interpretation of results on a more conceptual level, references to and percentage changes in the Time variable are given with respect to directly measured time intervals, not to the natural logarithms of those values. However, all p values presented in conjunction with the Time variable are those obtained from statistical analysis using the natural logarithm values. All interpretations of statistical significance or non-significance involving directly measured time scores are made with the assumption that any relationship involving the mean of the log of time scores will also hold for the corresponding relationship involving the arithmetic mean of direct time scores.

RESULTS

EFFECT OF AGE AND HAND ON FORCE CONTROL

Age as a main effect averaged over all other independent variables was significant for both Time [$F(2,27) = 4.04$, $p < 0.05$; $\eta^2 = 0.23$] and RMSE [$F(2,27) = 2.72$, $p < 0.05$; $\eta^2 = 0.28$]. As revealed in the *post hoc* comparisons the Y20 group was faster than the O80 group ($p < 0.05$) and more accurate than the O70 ($p < 0.05$) and O80 groups ($p < 0.05$).

These participants, young and old, did not exhibit a between-hand performance difference for time taken to complete the task. However, the Hand × Day interaction for RMSE was significant [$F(4,24) = 3.99$, $p < 0.05$; $\eta^2 = 0.40$]; with the right hand making lesser error, when compared to the left hand, on Days 2 and 3 ($p < 0.05$; **Figure 2**). The Hand × Segment interaction for RMSE was significant [$F(5,23) = 5.94$, $p < 0.01$; $\eta^2 = 0.56$] with the right hand making lesser error, when compared to the left hand on Segments 3–6 ($p < 0.05$; **Figure 3**).

The three-way interaction of Hand × Segment × Age [$F(10,46) = 3.27$, $p < 0.01$; $\eta^2 = 0.42$] for RMSE also was significant. The left hand of the Y20 demonstrated lesser error than the left hand of the O80 for Segments 1–4 ($p < 0.05$). Additionally, the right hand of the Y20 demonstrated fewer errors than the right hand of the O70 for Segment 3 ($p < 0.05$) and fewer errors than the right hand of the O80 for Segment 6 ($p < 0.05$).

EFFECT OF PRACTICE ON FORCE CONTROL

The Day main effect for Time [$F(4,24) = 32.60$, $p < 0.001$; $\eta^2 = 0.85$] and RMSE [$F(4,24) = 16.07$, $p < 0.001$; $\eta^2 = 0.65$] were significant. As revealed in the *post hoc* comparisons, the time taken to complete the task was longer on Day 1 compared to all other days ($p < 0.05$). Participants made more error on Day 1, compared to all other days ($p < 0.01$) and on Days 2 and 3 compared to Day 5 ($p < 0.05$). Age interacted with Day for Time [$F(8,48) = 3.44$, $p < 0.01$; $\eta^2 = 0.37$; **Figure 4**] such that the Y20 were faster than O80 only on Days 4 and 5 ($p < 0.05$).

EFFECT OF SEGMENT ON FORCE CONTROL

The Segment main effect was significant for both Time [$F(5,23) = 31.96$, $p < 0.001$; $\eta^2 = 0.87$] and RMSE [$F(5,23) = 19.49$, $p < 0.001$; $\eta^2 = 0.81$]. As revealed in the *post hoc* comparisons, participants performed slower and with more errors on segments requiring target contact or change in force direction (Segments 3 and 6) when compared to all other segments ($p < 0.01$; **Figure 5**).

EFFECT OF AGE ON THE ASYMMETRY INDEX

Manual asymmetry for time taken to complete the task, averaged over days and segments, was not significantly different among the three age groups. Additionally, there was no Age effect on RMSE and no Day × Age interaction for manual asymmetry.

The Segment × Age interaction for manual asymmetry was not significant for Time or RMSE when performance was averaged across days. However the Day × Segment × Age interaction for RMSE was significant [$F(40,16) = 2.63$, $p < 0.05$; $\eta^2 = 0.86$]. As revealed in *post hoc* comparisons, both the Y20 and the O70 groups were more asymmetric than the O80 group but only on Day 4, Segment 6 ($p < 0.01$ and $p < 0.05$, respectively).

EFFECT OF PRACTICE ON THE ASYMMETRY INDEX

Practice resulted in a significant decrease in manual asymmetry of time taken to complete the task [$F(4,24) = 2.77$, $p < 0.05$; $\eta^2 = 0.32$]. As revealed in *post hoc* comparisons, manual asymmetry for Time was lowest on Day 4 when compared to Days 1, 2, and 5 ($p < 0.01$). Practice had no significant effect on manual asymmetry of RMSE. In addition, the Day × Segment interaction was not significant for Time or RMSE.

EFFECT OF SEGMENT ON THE ASYMMETRY INDEX

The Segment main effect for manual asymmetry of time taken to complete the task was significant [$F(5,23) = 8.14$, $p < 0.001$; $\eta^2 = 0.64$]. As revealed in *post hoc* comparisons, manual asymmetry was greatest on Segments 3 and 6 ($p < 0.01$; **Figure 6**).

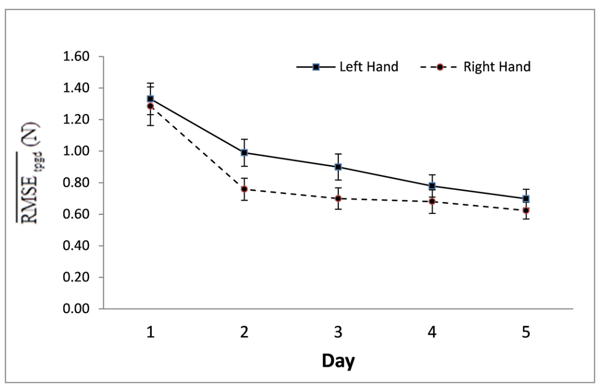

FIGURE 2 | Mean RMSE and standard errors of right and left hand performances by practice day as averaged over all segments (s) of all respective performance hand trials (t) of all participants (p) of all age groups (g). The mean RMSE scores of right vs. left hand performance were significantly different on Days 2 and 3 ($p < 0.05$).

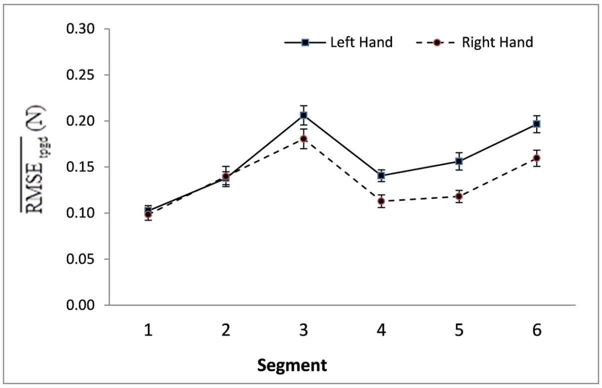

FIGURE 3 | Mean RMSE and standard errors of right and left hand performances by practice day as averaged over all segments (s) of all respective performance hand trials (t) of all participants (p) of all age groups (g). The mean RMSE scores of right vs. left hand performance were significantly different on Days 2 and 3 ($p < 0.05$).

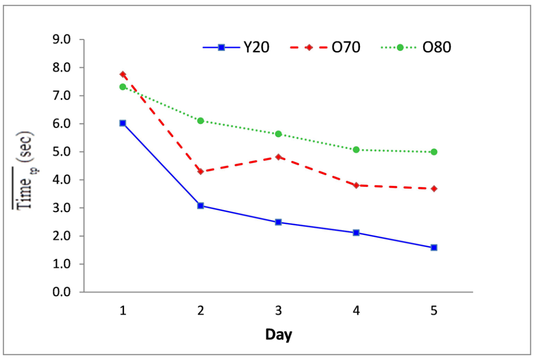

FIGURE 4 | Age group mean whole Task Time scores by practice day as averaged over all trials (t) of all participants (p). There was a statistically significant difference between the arithmetic mean time score for the Y20 vs. O80 groups on Days 4 and 5 ($p < 0.05$).

Proximity to the reverse circle (Segment 3) and end (Segment 6) had a powerful effect on manual asymmetry for time taken to transverse the different segments. The magnitude of manual asymmetry for RMSE, expressed across segments, did not change with practice.

DISCUSSION

Three main findings emerged from this study. First, we observed no inter-manual performance asymmetry on this isometric tracing task among any of the age groups, either in the hand performance differences or in the magnitude of the AI. Second, the Y20 and O70 group improved performance across the five days of practice although the O80 group did not and practice did not differentially affect the AI for the three age groups. Practice also differentially affected the accuracy of performance of the two hands. Third, all age groups exhibited poorer performance and larger AIs on the most difficult segments of the task (3 and 6) and this did not change with practice.

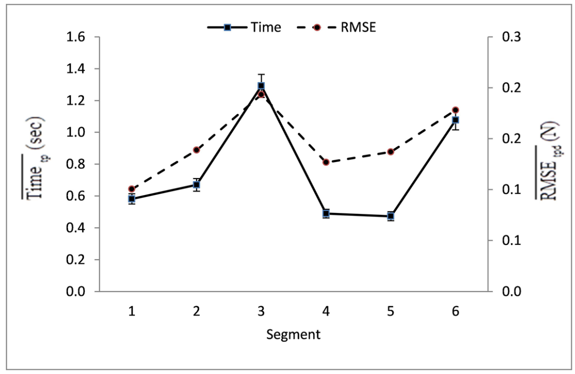

FIGURE 5 | Mean Task Time and standard errors by segment as averaged over all trials (t) of all participants (p) in all groups on all practice days (d). The arithmetic mean time and the mean RMSE score for Segments 3 and 6 have a statistically large significant difference from those mean scores of all other segments ($p < 0.01$).

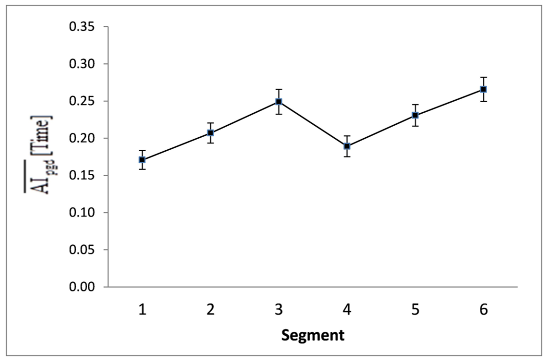

FIGURE 6 | Mean absolute asymmetry index and standard errors of the dependent variable *Time* for each of the six segments as averaged collectively over all participants (p) in every group (g) on every practice day (d). The mean AI time scores were significantly different on Segments 3 and 6 ($p < 0.05$).

AGE AND INTER-MANUAL PERFORMANCE ASYMMETRY

In this isometric force tracing task, there were no significant age differences in inter-manual performance asymmetry for time or accuracy, as evidenced by the lack of significant age interactions with any of the other study factors. If the HAROLD model were operative we would expect older adults to be less asymmetrical compared to young adults and if the Right Hemisphere Aging model were operative we would expect older adults to be more asymmetrical compared to young adults, even after five days of practice. The lack of age differences in asymmetry in this isometric tracing task are not explained by either model but may be related to the observations made by Paizis et al. (2014) who found age differences in inter-manual asymmetry that were based on whether the task required actual movements of the arms or imagined arm movements. Their older adults exhibited inter-manual asymmetry in actual pointing movements, but not during their imagined pointing movements. Thus, in both their study and the present study, inter-manual asymmetry was not seen when little or no movement occurred. Our findings suggest that planning, execution, and central processing of visuospatial feedback required for this isometric force tracing task were not negatively affected by age, even in the oldest age group. Our older adults showed no signs of age-related degradation of asymmetry. Our results provide yet another example that age changes in manual asymmetry are not global but rather, are task-specific (Chua et al., 1995; Francis and Spirduso, 2000; Seidler, 2007; Teixeira, 2008; Voelcker-Rehage, 2008). Isometric line tracing, which requires gradual increases and decreases at low force levels would fall in Teixeira's (2008) manual asymmetry category he designated as *symmetric* performance, rather than *inconsistent* or *asymmetric* performance.

One explanation for the symmetry observed in this task may be that isometric force line tracing can also be categorized as a dynamic visuospatial task accomplished with the muscle activity held at a fixed length. Movement tasks such as reaching and hand drawing require concentric muscular contractions (muscle activity shortening) and eccentric contractions (muscle activity lengthening) and multiple joint angle changes, all of which would provide additional sensory feedback processing (Proske and Gandevia, 2012). Other investigators using dynamic isometric force control tasks such as matching different force levels (Harabst et al., 2000), force-tracking sine waves (Voelcker-Rehage and Alberts, 2005), and randomly shaped templates (Lazarus and Haynes, 1997) reported age differences in inter-manual performance asymmetry, but it is likely that the cortical planning and execution for these tasks were more complex.

AGE AND PRACTICE EFFECTS ON INTER-MANUAL PERFORMANCE ASYMMETRY

Five days of practice decreased the amount of time taken to complete the task, but not similarly for all three groups, and the interaction of Age and Practice was significantly different only for time taken to complete the task, not for accuracy of performance (**Figure 4**). No age group differences were observed across the first 3 days of practice, but by Days 4 and 5 the young group completed the task significantly faster than the oldest group. In addition, both the Y20 and O70 were significantly faster than their own Time on Day 1 while the O80 group demonstrated no significant changes in time to complete the task across 5 days of practice. Our findings support the many studies that have shown that with practice both young and older adults improve in fine movement skills (e.g., Bock and Schneider, 2002; Kennedy and Raz, 2005; Rodrigue et al., 2005; Seidler, 2007; Voelcker-Rehage, 2008) and also in isometric force control tasks (Lazarus and Haynes, 1997; Voelcker-Rehage and Alberts, 2005; Poston et al., 2008; Camus et al., 2009; Sosnoff and Voudrie, 2009; Francis et al., 2012).

The largest practice-related changes in isometric tracing occurred in the O70 group from Days 1 to 2, a result that also occurred in two other studies: Poston et al. (2008) in an isometric force matching task and Voelcker-Rehage and Alberts (2005) in an isometric tracking study. However, our results do not agree with Christou et al. (2007) who reported that older adults approximately the same age as our O70 group performed a force matching task with time errors and endpoint accuracy errors similar to those of a young group after only 35 trials of practice. Our oldest group did not significantly decrease task time throughout 5 days of practice. Several other researchers of isometric force control have proposed that no matter how much older adults practiced, they could never close the age gap in tracking an irregular template pattern (Lazarus and Haynes, 1997; Voelcker-Rehage and Alberts, 2005), and index finger force matching (Sosnoff and Voudrie, 2009). These researchers suggested that older adults could not improve their processing of target-related sensorimotor feedback quickly enough, and could not reduce motor unit firing rate variability which has been shown to improve inter- and intra-muscle coordination (Laidlaw et al., 1999; Kamen and Knight, 2004; Griffin et al., 2009). Indeed, Pratt et al. (1994) provided evidence, and more recently Christou et al. (2007) revealed that in many cases even when older adults' performances appear not to be different from those of young adults, the mechanisms underlying the movements of older adults can be qualitatively different. In their study of isometric index finger abduction time and accuracy, they suggested that the age differences in target accuracy that disappeared after 35 practice trials were associated with timing adaptations of the agonist and antagonist balance of electromyographic (EMG) activity. Young adults adjusted both the agonist and antagonist EMG to improve force endpoint accuracy, whereas old adults adjusted only the agonist muscle EMG to improve force endpoint accuracy.

Unlike the significant age group differences in time over the 5 days of practice, none of our age groups decreased errors across days. This result is in contrast to that of Voelcker-Rehage and Alberts (2005) study whose participants, approximately the same age (67–75) as our O70 age group, were significantly less accurate as indicated by their ability to stay within a target range. The differing results could be because the isometric force matching task in the Voelcker-Rehage and Alberts (2005) study was a more difficult task differing from our task in at least three ways number of force direction reversals (12 vs. 2), length of task (30 vs. 10 s), and range of template peak force levels (2–5 vs. 6–11%). All of these differences would increase the difficulty level of their task, and it is well-documented that increasing difficulty level increases age decrements in fine motor tasks (Spirduso et al., 2005b).

The magnitude of AI for time changed with 5 days of practice but not for accuracy. However this finding was attributable to Day 4 only and there was no trend or evidence that the participants' hand performances were either systematically converging or diverging as a result of age or practice. Also, given the lack of a significant Age × Day interaction for error suggests that the change in AI was similar for the young and older groups across days.

Practice across 5 days had a differential effect on accuracy of the two hands. As revealed in the significant Hand × Day interaction for RMSE, the right and left hands, combined across age groups, erred in tracing the template erred in tracing the template almost identically on the first day, but the two hands diverged along different trajectory paths to arrive at almost identical mean error on the last day (**Figure 2**). The right hand of the combined age groups decreased mean error acutely from Day 1 to Day 2 and then plateaued, making almost no more decrease in mean error throughout the rest of the practice days. Conversely, the left hand mean error decreased more gradually, catching up to the right hand level of performance so that the two hands performed similarly on Day 4 and Day 5.

These results are partially consistent with those from studies of young adults in which right and left hands practiced anisometric (movement) tasks and the two hands that performed asymmetrically on initial trials converged to perform similarly after many trials of practice, as in finger tapping speed (Peters, 1976), finger dexterity (Perelle et al., 1981; Bryden and Allard, 1998), finger movement sequencing (Teixeira and Okazaki, 2007), and older adults in pegboard tests (Weller and Latimer-Sayer, 1985). Our results differed from their results primarily in the almost identical performance of the two hands on Day 1, rather than an asymmetrical performance which might be expected in a sample of self-reported right handers. Our task also differed from theirs in several important ways. The first is that the task used in the present study is an isometric force control task, which involves no movement and minimal consequent central processing of movement-generated feedback (Lazarus and Haynes, 1997). The second is that our participants were screened on Day 1 for their understanding of the task by two joystick trials on each hand. The third difference is that unlike the tasks used in other studies cited, this isometric tracing task is not one encountered in activities of daily living in which the right hand may have experienced unequal amounts of practice. Therefore the two hands may have found the task equally as novel on the first day, but the more dominant right hand acquired the skill more quickly and plateaued.

AGE AND TASK DIFFICULTY EFFECTS ON INTER-MANUAL PERFORMANCE ASYMMETRY

Task difficulty has been described as the level of complexity, (e.g., the portion of involved subsystems or abilities) that a task requires to complete it, or as "a skill that cannot be mastered in a single session, has more than one degree of freedom, and has the potential to be ecologically valid" (Wulf and Shea, 2002; Voelcker-Rehage, 2008, p. 64). The term *difficulty level* of a task has also been defined behaviorally by the time required to learn the task (Voelcker et al., 1999). In this study we presented a task requiring sustained applications and releases of isometric force, but introduced a change in difficulty in two locations along the tracing template, Segment 3 and Segment 6. The Segment main effect confirmed that these two segments took longer to navigate and generated larger mean error than the other four segments, confirming that within this task these two segments were more difficult for all age groups than the other four segments (**Figure 5**). Although the older groups tended to trace more slowly and make more errors, the age differences were not significant.

Inter-manual asymmetry were robustly different, however, beginning with Segment 3 and continuing through Segment 6 (**Figure 3**). The right hand (averaged across age groups) made fewer errors than the left hand on these last four segments. Thus, inter-manual asymmetry was more sensitive to changes in difficulty than the age factor was. Segment 3 is difficult because it requires the anticipation of a reversal of force direction (Spirduso et al., 2005b; Griffin et al., 2009; Eakin et al., 2012; Francis et al., 2012; Herring-Marler et al., 2014) approaching a target (Reverse Circle), requirements that are known to slow down the approach and induce errors (Salthouse, 1985). Segments 4 through 6 require the controlled release of force, known to be more difficult than controlled application of force which occurs in Segment 2 and Segment 3 (Spirduso and Choi, 1993).

Segment difficulty was also the most potent factor to affect the AI with regard to the time taken to complete the task (**Figure 6**). The difference between the performance of the hands was greater on Segment 3 and Segment 6, suggesting that the right hand completed the task more quickly than the left hand on the most difficult segments. It was not, however, more or less accurate than the left hand, indicating that a speed/accuracy tradeoff is not applicable.

In summary, old adults navigated the two most difficult segments as well as the young adults, as there were no interactions of age with segment or hand performance, either of inter-manual asymmetry or in the analysis of within-person AI. However, segment difficulty was a potent factor in the time taken by each hand to complete the task.

LIMITATIONS

There were limitations in the present investigation. First, it focused on a specific motor task, isometric pinch force, and the findings more likely would be related to other studies of isometric force control rather than anisometric tasks. Second, the results of our study can only be generalized to an adult population who passed a stringent health screening, are well-educated and highly motivated. Therefore, the observed effects of aging, on manual asymmetry and isometric pinch force acquisition, likely reflect a best-case scenario of successful aging rather than a typical course of change.

CONCLUSION

Results presented in this study show that when movement-generated feedback is absent or greatly reduced, as occurs in this isometric force control tasks, and when young and old participants are not time constrained, as occurs in tracing vs. tracking targets, age differences in inter-manual performance asymmetry are not found. These results do not support the HAROLD model but provide support for the notion that age and practice effects on asymmetry are task-specific. Practice effects depended on age level in that the Y20 and O70 groups improved performance by decreasing time taken to complete the task. However the O80 groups did not significantly improve with practice and practice did not significantly affect the AI for any age group. In addition, practice differentially affected the accuracy of performance of the two hands. Finally, all age groups exhibited poorer performance and larger AIs on the two most difficult segments (3 and 6) and this did not change with practice.

In conclusion, knowledge about isometric motor control in neurologically intact older adults is relevant to rehabilitation specialists such as physical therapists and occupational therapists who work with neuromuscularly impaired adults. Isometric tasks that can be performed by either hand and require very low levels of force are especially important tools for therapists working with patients attempting to recover from unilateral impairments in brain connectivity, such as stroke, fall-related concussions, or accidents.

ACKNOWLEDGMENTS

The authors would like to thank Kami Teal (Pepperdine University) for her assistance with data collection.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 30 September 2014; accepted: 23 December 2014; published online: 15 January 2015.

Citation: Francis KL, MacRae PG, Spirduso WW and Eakin T (2014) Age and practice effects on inter-manual performance asymmetry. Front. Psychol. ***5****:1585. doi: 10.3389/fpsyg.2014.01585*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 24 February 2015
doi: 10.3389/fpsyg.2015.00167

Exploring manual asymmetries during grasping: a dynamic causal modeling approach

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Recording of neural activity during grasping actions in macaques showed that grasp-related sensorimotor transformations are accomplished in a circuit constituted by the anterior part of the intraparietal sulcus (AIP), the ventral (F5) and the dorsal (F2) region of the premotor area. In humans, neuroimaging studies have revealed the existence of a similar circuit, involving the putative homolog of macaque areas AIP, F5, and F2. These studies have mainly considered grasping movements performed with the right dominant hand and only a few studies have measured brain activity associated with a movement performed with the left non-dominant hand. As a consequence of this gap, how the brain controls for grasping movement performed with the dominant and the non-dominant hand still represents an open question. A functional magnetic resonance imaging (fMRI) experiment has been conducted, and effective connectivity (dynamic causal modeling, DCM) was used to assess how connectivity among grasping-related areas is modulated by hand (i.e., left and right) during the execution of grasping movements toward a small object requiring precision grasping. Results underlined boosted inter-hemispheric couplings between dorsal premotor cortices during the execution of movements performed with the left rather than the right dominant hand. More specifically, they suggest that the dorsal premotor cortices may play a fundamental role in monitoring the configuration of fingers when grasping movements are performed by either the right and the left hand. This role becomes particularly evident when the hand less-skilled (i.e., the left hand) to perform such action is utilized. The results are discussed in light of recent theories put forward to explain how parieto-frontal connectivity is modulated by the execution of prehensile movements.

Keywords: reach-to-grasp, hand dominance, functional magnetic resonance imaging, dynamic causal modeling

INTRODUCTION

Human motor system organization is based on the principle of contralateral control of distal movement components, which is reflected at an anatomical level in a nearly complete cross-over of corticospinal fibers innervating distal muscles. It is known that the human brain is composed of two hemispheres that are not symmetrical, but specialized in some functions such as the motor control of the two hands. At the same time, right-hand dominance is considered evidence of a behavioral brain specialization, and 9 out of 10 individuals show a preference for right hand usage during most manual activities (Perelle and Ehrman, 1994). The question remains: how is right hand preference reflected in functional brain organization?

Recent neuroimaging techniques have made it possible to investigate the relationship between hand dominance and functional brain architecture. In this respect, functional magnetic resonance imaging (fMRI), electroencephalography (EEG), positron emission tomography (PET), magnetoencephalography (MEG), and transcranial magnetic stimulation (TMS) experiments have been recently utilized to study whether behavioral asymmetry (hand dominance) is associated with asymmetric neural tissue activation in the two hemispheres (Kim et al., 1993; Baraldi et al., 1999; Brouwer et al., 2001; Kobayashi et al., 2003; Pollok et al., 2006; Basso et al., 2006; Begliomini et al., 2008; Martin et al., 2011; Kourtis et al., 2014). Those studies have produced differing results in particular with regard to the activation of ipsilateral motor cortical areas in connection to the moving hand; the majority of fMRI studies has confirmed contralateral but also ipsilateral activation within motor-related areas (Kim et al., 1993; Baraldi et al., 1999; Kobayashi et al., 2003; Verstynen et al., 2005).

A point worth noting, however, is that it remains unclear whether activations are associated solely with higher order cortical areas and whether they regard only the non-dominant hand. Some studies report that hemispheric asymmetries in ipsilateral activations are present at the level of primary motor cortex (M1; Kawashima et al., 1993; Kim et al., 1993; Babiloni et al., 2003). Other studies seem to suggest that greater or lesser activation in the ipsilateral motor cortex is similar during left- or right-hand movements (Volkmann et al., 1998) and attribute hand dominance to a possible hemispheric asymmetry of higher order motor cortices such as premotor or supplementary motor areas (Hlustík et al., 2002). Despite the fact that the extent and magnitude of activation were found to be greater in the hemisphere contralateral to the hand being used (Culham and Valyear, 2006; Begliomini et al., 2008), recent fMRI evidence suggests that in right-handers grasping with either hand led to activation in the bilateral anterior intraparietal sulcus (AIP) and the right dorsal premotor cortex (dPMC; Begliomini et al., 2008). In this scenario, the control processes underlying hand dominance remain controversial for skilled movements. In part, this might be due to the measures used to identify unique attributes of the two hemispheres. Amongst these, the region of interest (ROI) method usually circumscribes the analysis to *a priori* defined brain regions within the left and the right hemispheres. As revealed by several studies, the precise localization of particular areas may vary across subjects (see Volkmann et al., 1998; Verstynen et al., 2005) and their anatomical size may differ across the left and right hemispheres (Amunts et al., 1996, 2000). The adoption of the ROI approach, thus, might represent a potential confound as it would run the risk of comparing regions that are functionally not quite equivalent in different individuals and different hemispheres.

With this in mind, here we considered the idea that the two hemispheres might contribute in different ways to the execution of grasping movements performed either with the left or the right hand. And to test this, we adopted the Dynamical Causal Modeling approach (DCM – Friston et al., 2003). DCM belongs to the family of effective connectivity approaches and has the potentiality of inferring about causality regulating functional couplings among brain regions. In our case, this peculiarity represents a potential key to disentangle a possible diverse contribution of the two hemispheres while performing grasping movements with the left or the right hand. We used DCM on fMRI time series (Friston et al., 2003) acquired during the execution of visually guided reaching-to-grasp movements toward a spherical object evoking precision grasping. This approach gives us the possibility to explore the inter-regional couplings between the main areas characterizing the grasping circuit in humans, that is the AIP together with the ventral premotor cortex (vPMC), the dPMC, and the M1 (Castiello, 2005; Castiello and Begliomini, 2008; Filimon, 2010).

Therefore the central aim of the present study was to verify whether, in right-handers, the execution of precision grip movements with either hand recruits the grasping circuit in a specular way [e.g., grasping with the right dominant hand (RDH) mainly recruits the left hemisphere and grasping with the left non-dominant hand (LNH) mainly recruits the right hemisphere] or whether hand dominance (i.e., RDH or LNH) could represent a crucial aspect for connectivity patterns among areas belonging to the grasping circuit. From this perspective, on the basis of available literature on both structural and functional data in both humans and monkeys (see **Table 1**), we hypothesized that the execution of precision grip movements with the LNH could modulate the connection between AIP areas of both hemispheres with respect to precision grip movements performed with the RDH. In fact, many studies have demonstrated bilateral AIP involvement when precision grip movements are performed with the dominant hand (Culham and Valyear, 2006; Davare et al., 2006, 2007). Since the left hand is less skilled, especially in performing precision movements (Gonzalez et al., 2006), we hypothesize that the execution of such movements with a not-skilled hand may require additional visuomotor processing, which could be provided by the contribution of both AIP areas. Alternatively, we hypothesized that, according to the model suggested by Rizzolatti and Luppino (2001), emphasizing the role of the connection AIP-vPMC in visuo-motor transformation underlying grasping movements, the connections between vPMCs could be 'affected' by precision grip movements performed with the LNH (see **Table 1**). Another plausible scenario could be represented by the possibility that the dPMC could be modulated by the execution of a precision grip movements performed with the LNH with respect to precision grip movements performed with the RDH, given the additional on-line control required by the execution of precision movements with the non-dominant hand (Begliomini et al., 2008). Finally, we also considered the hypothesis that the execution of a precision grip movement with the LNH does not modulate brain activity within the ipsilateral left hemisphere until execution. In this view, it might well be that it is the connection between the two primary motor areas to be modulated by the execution of a precision grip movement performed with the LNH.

To summarize, the study focusses on the potential role played by hand dominance in the modulation of inter-hemispheric connections between homologs areas. In particular, on the basis of findings collected by previous studies from ours and other groups (Gonzalez et al., 2006, 2007; Begliomini et al., 2008 – see **Table 1**), we hypothesize that the execution of precision grip movements performed with the LNH could rely on the contribution of both hemispheres. Therefore, two possible main scenarios were considered (**Figure 1**):

(1) the execution of precision grip movements performed with the RDH modulates inter-hemispheric connections between homologs areas (models #1–4);

Table 1 | Studies supporting the existence of inter-hemispheric connections between grasping areas.

Connection	Non-human primate studies	Human primate studies
AIP – AIP		Tunik et al. (2005), Culham et al. (2006), Rice et al. (2006), Davare et al. (2007), Begliomini et al. (2008), Le et al. (2014)
vPMC – vPMC	Boussaoud (1995), Dancause et al. (2007)	
dPMC – dPMC	Marconi et al. (2003)	Begliomini et al. (2008)
MI – MI	Jenny (1979), Leichnetz (1986), Rouiller et al. (1994)	Davare et al. (2007)

AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex.

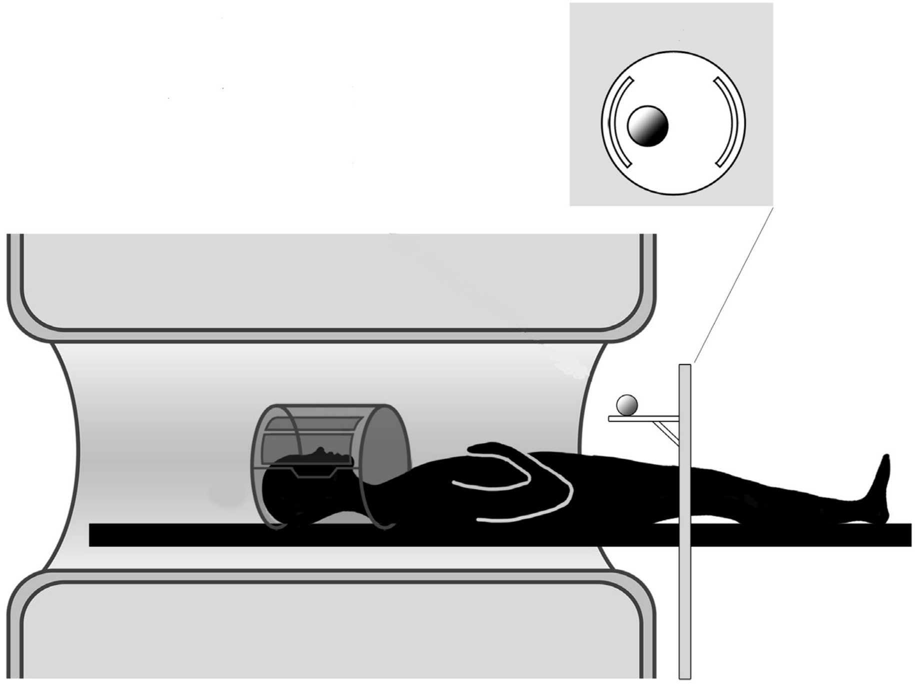

FIGURE 1 | Experimental setup. The participant is lying in the MR scanner and the motorized platform ABRAM is presenting stimuli following a sequence administered by a PC located in the control room. The position of the rotating platform plus a pillow slightly tilting the head allow for direct viewing of the stimuli.

(2) the execution of precision grip movements performed with the LNH modulates inter-hemispheric connections between homologs areas (models #5–8);

The crucial point of the study is to examine which of the region/s belonging to the grasping circuit is/are involved by a hypothetical 'encroachment' to the ipsilateral hemisphere and therefore which aspect of grasping movement execution requires 'additional' resources to be provided by the ipsilateral hemisphere.

MATERIALS AND METHODS

PARTICIPANTS

Eighteen right-handed subjects (11 women and 7 men; age range: 19–30 years; mean age: 24.7 years) participated in the experiment. They all had normal or corrected-to-normal vision, and they had no neurologic or psychiatric history, or any motor pathology. Hand dominance was assessed by means of the Edinburgh Handedness Inventory (Oldfield, 1971). On the basis of the scores obtained with this test all participants were classified as strongly right-handed (36/36). Before entering the scanner room all participants underwent MR safety screening and gave informed written consent according to the guidelines provided by the Declaration of Helsinki. The study was approved by the local Ethics Committee.

EXPERIMENTAL STIMULUS

The adopted stimulus consisted of a spherical plastic objects of 3 cm diameter presented at a constant distance of 30 cm. We used a regular geometric shape in order to make comparisons with macaque neurophysiology studies possible (Gallese et al., 1994; Umilta et al., 2007) and with the purpose to avoid confounds related to tool use, which is known to involve a particular network in the left-hemisphere (Johnson-Frey et al., 2005). The considered stimulus dimension was chosen to elicit a precision grip, which considers the opposition of thumb and index finger. The present investigation is confined to this kind of prehensile action since it has been well characterized in both neural (Ehrsson et al., 2001; Frey et al., 2005; Culham and Valyear, 2006; Begliomini et al., 2007a, 2014; Turella and Lingnau, 2014) and behavioral terms (e.g., Castiello et al., 1993; Jeannerod, 1981, 1984; Savelsbergh et al., 1996; Cuijpers et al., 2004; see Smeets and Brenner, 1999 for a review). Further, its accuracy requirements make it an ideal experimental framework to bold out the processes underlying planning and execution during grasping movements. With specific reference to neuroimaging studies, activation patterns registered during precision grip planning and execution appear to be characterized by a larger involvement of the parieto-frontal network with respect to other types of grasping movements (e.g., whole hand grasp – Begliomini et al., 2007a,b; see Filimon, 2010 for a review).

EXPERIMENTAL SETUP

The stimulus was presented by means of an MR compatible motorized circular rotating table (ABRAM1; **Figure 1**). The participants' upper arms were restrained with an elastic band to further minimize head movements consequent to arm movements. In order to keep the hand's starting position constant across all participants and trials, the participants were asked to wear a metal-free belt cushioned by a pad and instructed to keep the performing hand (right or left) in a relaxed position with the palm placed face down on the pad. The other upper arm/hand unit was strapped to the scanner bore. Supported by a foam wedge, the participant's head was tilted at an angle (~30°) to permit him/her to directly view the stimuli below the coil without needing mirrors; we were able, as a result, to avoid making other modifications that would have been required if mirror-viewing had been necessary (Culham et al., 2003; Cavina-Pratesi et al., 2007). While the participants were allowed to look freely between trials, they were explicitly instructed to look at the object throughout action execution.

TASK PROCEDURES

The participants were requested to grasp the object, depending on the signal that was given, with either the RDH or the LNH hand using a precision grip. The participants were asked to grasp the object at a natural speed, depending on a sound (right hand: low tone – duration: 200 ms; frequency: 1,7 kHz; left hand: high tone – duration: 200 ms; frequency: 210 Hz.) delivered by means of pneumatic MR-compatible headphones wore by participants. Although the object was at all times visible, the participants was instructed to begin the movement only upon hearing the sound. An operator in the control cabin next to the scanner room monitored the entire experiment. In particular, she checked that the participants fulfilled the task requirements in terms of grasping actions.

EXPERIMENTAL DESIGN

The experiment was conducted by using a mixed event-related design. The performing hand (RDH, LNH) was manipulated within runs as within-subjects factor. Trials to be performed with the same hand were grouped in sequences varying from four to eight elements. This was done in order to minimize brain activity due to frequent task changes (Culham et al., 2003). In accordance with a 'long exponential' probability distribution, the inter-stimulus interval (ISI), which was randomized across trials, varied from 3 to 8 s (Hagberg et al., 2001). An entire experimental session consisted of 120 trials, which were divided into two runs (kept short to minimize participants' fatigue) of 60 trials each per condition.

IMAGING PARAMETERS

Images were acquired by means of a whole-body 1.5 Tesla scanner (Siemens Magnetom Avanto) equipped with a standard Siemens coil (eight channels). Functional images were acquired with a gradient-echo, echo-planar (EPI) T2*-weighted sequence in order to detect blood oxygenation level-dependent (BOLD) contrast throughout the whole brain (37 axial slices acquired continuously with descending order, 56 × 64 voxels, 3 mm × 3 mm × 3.3 mm resolution, FOV = 196 mm × 224 mm, flip angle = 90°, TE = 49 ms). 114 volumes were collected continuously in each single scanning run (TR: 3 s), resulting in two functional runs of 5 m and 42 s duration (11 m and 24 s of acquisition time in all). High-resolution T1-weighted anatomical image was acquired for each participant (3DMP-RAGE, 176 axial slices, no interslice gap, data matrix 256 × 256, 1 mm isotropic voxel, TR = 1900 ms, TE = 2.91 ms, flip angle = 15°).

DATA ANALYSIS

Data preprocessing

Functional data were spatially pre-processed and analyzed with SPM8 (Statistical Parametric Mapping[1]). The first four scans for each session were discarded from data analysis to avoid effects due to the non-equilibrium state of magnetization. For each participant, the time series for each voxel was realigned temporally to acquisition of the middle slice and underwent motion correction, realigning each volume to the first in the series. The anatomical scan was then co-registered to the mean of all functional images, previously corrected for intensity inhomogeneities through the bias correction algorithm implemented in SPM8. EPI images were then normalized according to the MNI152 template, supplied by the Montreal Neurological Institute[2] and distributed with the software SPM8. Finally, images were smoothed using a 6 mm× 6 mm× 6.6 mm FWHM 3D Gaussian kernel (twice the native voxel size). After motion correction two participants had to be excluded from further analysis because of large head motion (exceeding voxel size, 4 mm).

General linear model

At the first level, for each single participant, movements performed either with the RDH or the LNH were modeled as separate regressors with a General Linear Model (GLM - Friston et al., 1995). The duration of the movement was assumed of about 1.5 s on the basis of behavioral observations before the experimental session, done in order to get participants acquainted with the experimental setup. Regressors were defined on the timing of presentation of each experimental condition (cueing sound). These functions were convolved with a canonical, synthetic haemodynamic response function (HRF) plus temporal derivative to produce individual models (Henson et al., 2001). For each subject, both regressors were incorporated into General Linear Models (Holmes et al., 1997). Further, motion correction parameters, created during the realignment stage, missed trials, errors as well as the remaining part of the movement (the hand going back from the object to the starting position) were included in the analysis as a covariate of no interest. This was done in order to model residual effects due to head motion and factors of no interest. Individual models were separately estimated and contrasts were defined in order to pick out the main effects of each experimental condition. Time series data were concatenated over the sessions, and two regressors of no interest were added to the model to account for session effects.

DCM models

The question that the DCM tries to address in this study is concerned with the hypothesis that precision grip movements performed with the RDH or the LNH could modulate interhemispheric connections between homologous areas (e.g., right AIP–left AIP) in different ways, according to the models described in **Figure 2**.

[1] www.fil.ion.ucl.ac.uk/spm
[2] http://www.mni.mcgill.ca

We hypothesized intra- and inter-hemispheric connections among the grasping key regions (AIP, vPMC, dPMC, and M1) on the basis of results obtained by single cell recordings performed on macaque monkeys (see **Table 1**) and referring to the model described by Castiello and Begliomini (2008). More in detail, whereas for inter-hemispheric connections between dPMC, vPMC, and M1 we can rely on neurophysiological data, concerning AIP we mainly refer to the results obtained in humans by means of neuroimaging techniques such as fMRI (Culham et al., 2006; Begliomini et al., 2008) and TMS – (Tunik et al., 2005; Rice et al., 2006; Le et al., 2014). Overall these studies seem to converge on the hypothesis of a bilateral contribution of AIP to grasping execution.

For each participant eight different models, considering eight different connectivity hypothesis were tested (see **Figure 2**). We considered anatomical models consisting of volumes of interest (VOIs) with reciprocal connections between them (DCM-A matrix) according to the considered theoretical model (Castiello and Begliomini, 2008). The visuomotor analysis of the to be grasped object served as driving input (matrix C), and therefore we considered AIP as the driving input area in each hemisphere, given its crucial role in such processes (Binkofski et al., 1998, 1999; Frey et al., 2005; Rice et al., 2006, 2007; Begliomini et al., 2007a). In our models, we did exclude any hypothesis related to stimulus-response coupling dynamics (sound → performing hand) since the present work focuses on grasping execution rather than planning.

According to our reference model (Castiello and Begliomini, 2008), the modulation induced by our experimental task is supposed to propagate through connections from AIP to vPMC, and from vPMC to dPMC. The subsequent connection is supposed to link dPMC with ipsilateral M1, which is assumed to be the final node of our models (see **Figure 2**). The performing hand (RDH; LNH – DCM-B matrix) served as a modulatory influence on the forward connections. We adopted the models #1–4 as 'RDH' family model since they do hypothesize inter-hemispheric interaction between homologous areas as driven by precision grip movements performed with the RDH (model #1: left AIP ↔ right AIP; model #2: left vPMC ↔ right vPMC; model #3: left dPMC ↔ right dPMC; model #4 left M1 ↔ right M1). Similarly, models #5, #6, #7, and #8 hypothesize the same structure, where the inter-hemispherical connection between homologous areas is modulated by precision grip movements performed with the LNH ('LNH' family; model #5: right AIP ↔ left AIP; model #6: right vPMC ↔ left vPMC; model #7: right dPMC ↔ left dPMC; model #8 right M1 ↔ left M1).

VOI definition

The relevant time series of the regions included in the DCM analysis were extracted from the fMRI data of each individual subject on the basis of event-related analyses in the context of the General Linear Model. The VOIs were both functionally and anatomically located: (i) for each participant, the *t-contrast* testing for the global effect of the experimental manipulation (precision grip movements performed with RDH + precision grip movements performed with LNH) was considered ($p < 0.001$, uncorrected for multiple comparisons); (ii) this contrast was inclusively masked

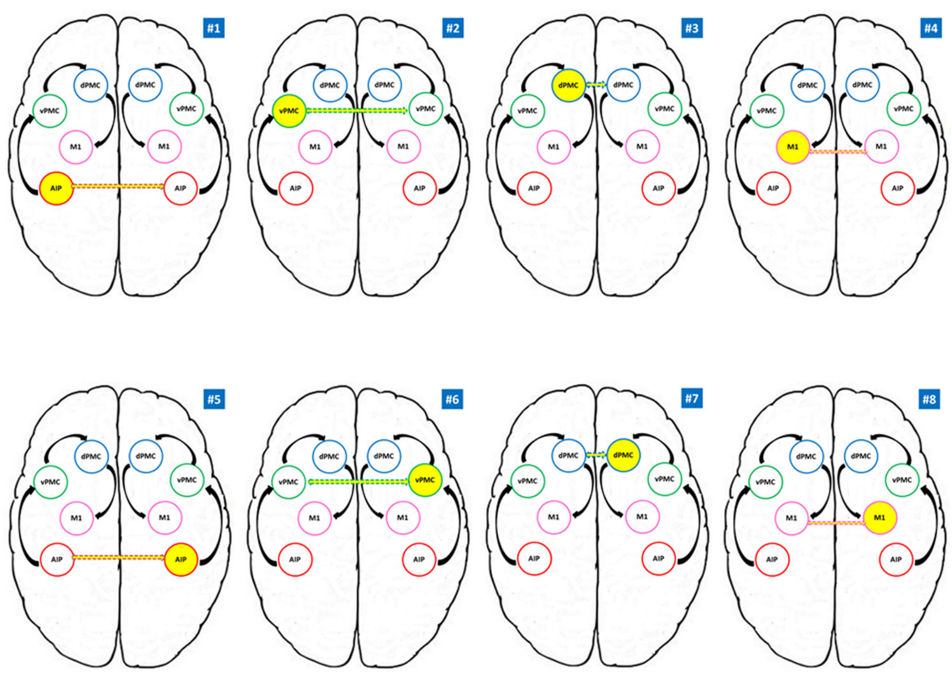

FIGURE 2 | Models tested for the RFX Bayesian Model Selection (BMS). AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex. Models #1 to #4 belong to the RDH family; models #5 to #8 refer to the LNH family. Yellow circles indicate the modulating region while dotted arrows indicate the connection to the homologous region in the other hemisphere. Black arrows indicate the intra-hemispheric structure of the model.

by the image resulting from the overlap *between* activation maps detected for each precision grip movement. This procedure was chosen in order to detect brain regions commonly involved by both movement without applying any statistical threshold; (iii) The small volume correction (Worsley et al., 1996) was performed on the resulting masked activation image by adopting the cytoarchitectonic maps provided by the toolbox Anatomy (Eickhoff et al., 2007) as searching areas. The following maps were selected: anterior intraparietal sulcus (Choi et al., 2006; Scheperjans et al., 2008), Broca's region (Amunts et al., 1999), the motor cortex (Geyer et al., 1996), and the premotor cortex (Geyer, 2003). The first set of coordinates detected for each area (AIP left, AIP right, vPMC left, vPMC right, dPMC left, dPMC right, M1 left, and M1 right) was chosen as the reference for the creation of the VOI. More in detail for M1 VOIs the chosen coordinate had to be located in the precentral gyrus, near the 'hand knob' (Yousry et al., 1997) while for the dPMC coordinates provided by Davare et al. (2006) were taken as a reference point to define the dorsal region of the premotor cortex. For each participant, a spherical VOI of 5 mm radius was built around the first set of coordinates detected with the SVC procedure in each of all the eight regions included in the analysis. The time series for each VOI was extracted by considering the 'effects of interest' (*t-contrast*) and adjusted for the 'effects of no interest' (*F-contrast*), including regressors of no interest (motion parameters, errors, missed trials, and time intervals needed by the hand to go back to the starting position after the movement). The percentage of variance observed for each regions was above 75% in all cases.

Model estimation and selection

In order to verify our hypothesis concerning laterality of the involvement of grasping areas during precision grip movements performed with the LNH and the RDH, we applied Bayesian inference to the hypothesized models (Penny et al., 2004). Bayes factors (i.e., ratios of model evidences) were used to compare different models. The estimated models were compared, based on the model evidences $p\,(y|\,m)$, which is the probability p of obtaining observed data y given by a particular model m (Friston et al., 2003; Stephan et al., 2009). Bayesian model selection (BMS) was performed with a random effects analysis using a Gibbs sampling method (Stephan et al., 2009; Penny et al., 2010). This method accounts for the possibility that different models apply to different subjects. Model comparison was (i) first done at the level of model families, i.e., subsets of models that share particular attributes. Two different model families were created, defined on the basis of the modulation hypothesis of connections (RDH-driven or LNH-driven). After that, (ii) we focused on the winning family considering the most significant modulation effect induced by our task.

The selection of a model yields the exceedance probability for each model family/model, which express the probability (in %) that a particular family/model is more likely than any other. Exceedance probabilities for all families/models sum to 100%.

RESULTS

GLM GROUP ANALYSIS RESULTS

Prior to conducting the DCM analyses described above, a conventional second-level Random Effect Analysis (RFX) was conducted on the HRF for the whole brain volume ($p < 0.005$, *FDR-corrected* for multiple comparisons, $k > 12$) as to confirm the involvement of motor, premotor, and parietal regions in our task. The contrast of interest tested for specific effects of precision grip movements performed with the RDH or with the LNH. These contrasts identified activation of cortical areas consisting of primary motor and premotor cortices, as well as parietal areas (see **Table 2**). In particular, while activity associated with precision grip movements performed with the RDH appeared to be more circumscribed to the left contralateral hemisphere, activity observed for precision grip movements performed with the LNH involved dorsal premotor and parietal regions of both hemispheres. The group analysis did not reveal any significant activity in the left vPMC, which was observed by means of a small volume correction (Worsley et al., 1996) instead. As described in the 'VOI definition' section, the VOIs were located for each participant following both functional and anatomical criteria. This procedure ensured that the functional regions included in the DCM models were as consistent as possible across subjects (Stephan et al., 2007; Seghier et al., 2011). Coordinates for each single region in each participant are reported in Table 1 of the Supplementary Material. No significant effects were observed for the same analysis procedure conducted on the time derivative included in the GLM model.

DCM RESULTS

Effective connectivity was tested by DCM-10, implemented in SPM8 toolbox (Wellcome Department of Imaging Neuroscience, London, UK), running under Matlab R2011a (The MathWorks, Natick, MA, USA).

Family wise results

Bayesian Model Selection was used first to decide which family model (RDH or LNH) better explains the measured data. The results showed that the 'LNH' family had an exceedance probability of 0.8902 compared to the 'RDH' family (0.1098; see **Figure 3A**). The winner family contains four models hypothesizing inter-hemispheric connections between homologs areas (AIP, vPMC, dPMC, and M1) as 'influenced' by precision grip movements performed with the LNH, which assumes that the modulation of connections starts from the right hemisphere.

Model-wise results

As a second step, we performed a RFX analysis on the four models belonging to the 'LNH' family and, as reported in **Figure 3B**, the 'dPMC' model is associated with the highest exceedance probability (0.847), followed by the 'M1' model (0.108) and the 'vPMC' model (0.029). The probability value associated with the 'AIP' model was even below 5% (0.014). This result indicates that, among the models we considered in the study, the 'winner' is characterized by bidirectional connections between dPMC areas of the two hemispheres.

In order to further characterize the peculiarities of the modulation induced on the connections of the winner model, parameter estimates resulting from Bayesian Model Averaging (BMA) were extracted for each connection of the models belonging to the winning family and were tested against 0 (one-sample t-test, $p < 0.05$)

Table 2 | Results of the RFX analysis performed on the whole group ($p < 0.005$, FDR-corrected for multiple comparisons, $k > 12$).

Cluster level			Peak level				MNI					
p(FWE)	*k*	*p(unc)*	*p(FDR)*	*t*	*Z-score*	*p(unc)*	*X*	*Y*	*Z*	*Side*	*Region*	*BA*
0.000	**1339**	**0.000**	**0.000**	**10.711**	**6.821**	**0.000**	**−48**	**−69**	**7**	**L**	**MTG**	**39**
			0.000	8.567	6.047	0.000	−55	−56	16	L	STG	22
			0.000	6.903	5.300	0.000	14	−72	22	R	PRECU	31
0.000	**347**	**0.000**	**0.000**	**10.478**	**6.746**	**0.000**	**−35**	**−20**	**64**	**L**	**PRECG**	**4**
			0.000	8.716	6.107	0.000	−38	−13	58	L	PRECG	6
			0.000	7.760	5.704	0.000	−42	−39	58	L	IPL	40
0.000	**651**	**0.000**	**0.000**	**9.415**	**6.375**	**0.000**	**41**	**−20**	**49**	**R**	**PRECG**	**4**
			0.000	8.051	5.832	0.000	47	−13	52	R	PRECG	4
			0.000	7.873	5.754	0.000	41	−13	58	R	PRECG	6
0.030	**32**	**0.008**	**0.000**	**7.033**	**5.364**	**0.000**	**11**	**7**	**−11**	**R**	**PUTAMEN**	
			0.002	4.435	3.858	0.000	21	13	−11	R	PUTAMEN	
0.016	**39**	**0.004**	**0.000**	**6.633**	**5.164**	**0.000**	**28**	**−56**	**55**	**R**	**SPL**	**7**
0.000	**125**	**0.000**	**0.000**	**6.469**	**5.079**	**0.000**	**54**	**−66**	**1**	**R**	**MTG**	**37**
			0.001	5.248	4.386	0.000	54	−63	19	R	STG	39
0.034	**31**	**0.009**	**0.000**	**5.818**	**4.723**	**0.000**	**21**	**−79**	**46**	**R**	**PRECU**	**7**
0.107	**20**	**0.029**	**0.002**	**4.513**	**3.911**	**0.000**	**−42**	**−30**	**31**	**L**	**POCG**	**2**
0.239	**13**	**0.071**	**0.001**	**5.039**	**4.256**	**0.000**	**51**	**0**	**25**	**R**	**IFG**	**9**
0.037	**30**	**0.010**	**0.001**	**5.008**	**4.236**	**0.000**	**44**	**−3**	**7**	**R**	**INSULA**	**13**
			0.005	3.847	3.441	0.000	51	10	10	R	IFG	44
0.107	**20**	**0.029**	**0.001**	**4.964**	**4.208**	**0.000**	**21**	**−6**	**10**	**R**	**GL. PALLIDUS**	
0.239	**13**	**0.071**	**0.002**	**4.481**	**3.890**	**0.000**	**8**	**−59**	**−35**	**R**	**CEREBELLUM**	
0.304	**15**	**0.093**	**0.002**	**4.386**	**3.825**	**0.000**	**21**	**−46**	**−47**	**R**	**CEREBELLUM**	
0.079	**12**	**0.451**	**0.090**	**3.791**	**3.399**	**0.000**	**−48**	**17**	**−2**	**L**	**IFG***	**45**
			0.090	3.425	3.121	0.001	−52	20	−5	L	IFG*	45

*The considered contrast is precision grip_RDH + precision grip_LNH. MTG, middle temporal gyrus; STG, superior temporal gyrus; PRECU, precuneus; PRECG, precentral gyrus; IPL, inferior parietal lobule; SPL, superior parietal lobule; POCG, post central gyrus; IFG, inferior frontal gyrus. Bolded font indicates the first activation peak of the cluster (in terms of t and Z score). *results obtained by means of a small volume correction.*

to verify whether a significant modulation was present. The results are reported in **Table 3** and depicted in **Figure 4A**. The statistical analysis revealed that grasping with both hands significantly modulated the selected input regions (namely AIP left for precision grip movements performed with RDH $t_{(15)} = 5.465$ $p < 0.000$, and AIP right for precision grip movements performed with the LNH, $t_{(15)} = 5.788$ $p < 0.000$). Concerning the left hemisphere, which is supposed to be primarily involved in the control of precision grip movements performed with the RDH (**Figure 4A**) the connections AIP-vPMC and vPMC-dPMC appeared as significantly modulated [namely $t_{(15)} = 3.649$ $p = 0.002$; $t_{(15)} = 2.686$ $p = 0.017$]. The connection between dPMC and M1 did not show any significant modulation effect. Concerning the right hemisphere, which is supposed to be primarily involved in the control of precision grip movements performed with the LNH (**Figure 4A**), the connections AIP-vPMC as well as vPMC-dPMC are significantly modulated, similarly to the left hemisphere [$t_{(15)} = 2.815$, $p = 0.013$; $t_{(15)} = 2.820$, $p = 0.013$]. Also for the right hemisphere, the dPMC-M1 connection did not appear as significantly modulated. When looking at inter-hemispheric connections between homologous areas (**Table 4**; **Figure 4B**), the connection between AIPs appears to be significantly modulated in the L → R direction but not viceversa [$t_{(15)} = 2.563$, $p = 0.022$ vs. $t_{(15)} = 1.705$ $p = 0.109$]. Concerning dPMC, the connection appears to be modulated in both directions (L → R $t_{(15)} = 2.158$, $p = 0.048$; R → L $t_{(15)} = 2.801$, $p = 0.013$]. No further significant results were observed concerning analysis performed on individual connections.

More in detail, paired t-tests were also conducted to test for differences between inter-hemispheric connections, in order to examine more in depth the results highlighted by the BMA. The results (**Tables 4A,B**) show that connections from the left toward the right hemisphere do not differ in terms of strength. It is worth mentioning that the modulation exhibited from the dPMC_LEFT toward the dPMC_RIGHT almost reaches significance with respect to all the other considered LEFT → RIGHT connections [dPMC-AIP: $t_{(15)} = -2.119$, $p = 0.051$; dPMC-vPMC: $t_{(15)} = -2.116$,.051; $t_{(15)} = 2.089$,

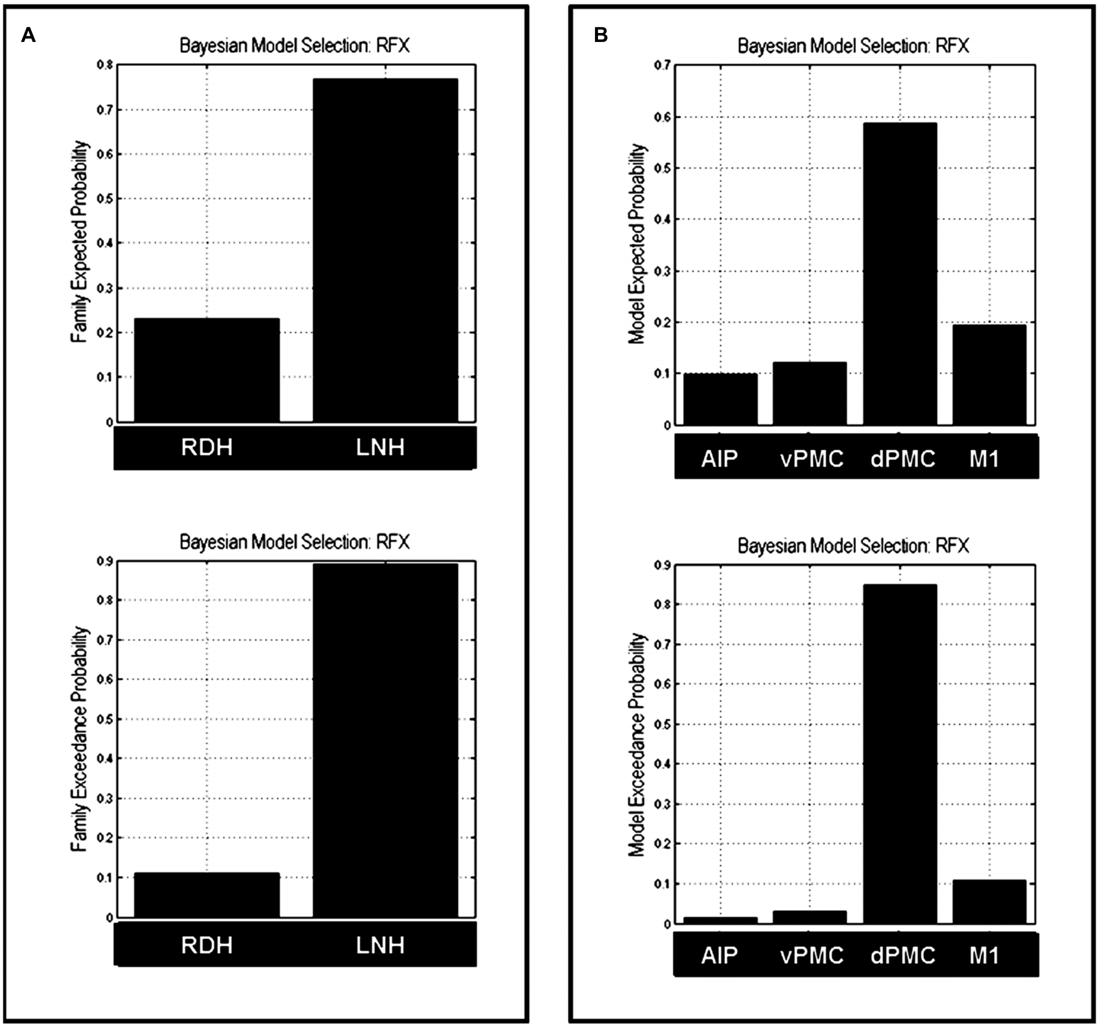

FIGURE 3 | Results of the BMS RFX performed at the family level (A) and at the model level (B). For both levels, expected (upper panels) and exceedance probabilities (lower panels) are reported. RDH, right dominant hand; LNH, left non-dominant hand; AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex.

$p = 0.054$]. Differently, when looking at RIGHT → LEFT connections, the modulation effect exhibited by the connection between dPMC areas significantly differs from the others (dPMC-AIP: $t_{(15)} = -2.758$, $p = 0.015$; dPMC-M1: $t_{(15)} = -2.765$, $p = 0.014$; $t_{(15)} = -2.804$, $p = 0.013$]. No further significant effects were observed.

DISCUSSION

We used DCM to evaluate whether and how the intra- and inter-hemispheric couplings between brain areas composing the parieto-frontal network underlying grasping movements were modulated by the used hand. To test this hypothesis, right-handed participants were requested to perform reach to grasp movements toward and grasp an object with either the right or the left hand. The relative simplicity of the motor task enabled us to obtain robust coupling parameters between key areas of the grasping circuit.

In general, we showed that when right-handers perform a precision grip movement with the RDH it is the left hemisphere to be chiefly involved. However, when they perform a precision grip movement with the LNH the ipsilateral hemisphere is also involved. More specifically, such involvement appears to be confined at the level of the dPMC and to a lesser extent at the level of the AIP and the vPMC.

Some functional imaging studies in which neurovascular responses that were evoked during visually guided grasping movements by right-handers were localized, demonstrated that there was increased activity in the region situated between the intraparietal and the inferior postcentral sulci (AIP; ; Toni et al., 2001; Culham et al., 2003; Begliomini et al., 2007a, 2008) and in the ventral portion of the precentral gyrus (vPMC; Toni et al., 2001). Similar activities were also noted during object manipulation studies (Binkofski et al., 1999; Ehrsson et al., 2000; Johnson-Frey et al., 2005).

Table 3 | Results obtained by one-sample t-tests performed on the parameter estimates related to input effects, inter-regional, and modulatory connections of the winning family LNH ($p < 0.05$).

	INPUT	AIP LEFT	AIP RIGHT	vPMC LEFT	vPMC RIGHT	dPMC LEFT	dPMC RIGHT	M1 LEFT	M1 RIGHT
AIP LEFT	$t_{(15)} = 5.465$ $\boldsymbol{p < 0.000}$		$t_{(15)} = 1.705$ $p = 0.109$						
AIP RIGHT	$t_{(15)} = 5.788$ $\boldsymbol{p < 0.000}$	$t_{(15)} = 2.563$ $\boldsymbol{p = 0.022}$							
vPMC LEFT		$t_{(15)} = 3.649$ $\boldsymbol{p = 0.002}$			$t_{(15)} = 1.929$ $p = 0.073$				
vPMC RIGHT			$t_{(15)} = 2.815$ $\boldsymbol{p = 0.013}$	$t_{(15)} = 1.946$ 0.071					
dPMC LEFT				$t_{(15)} = 2.686$ $\boldsymbol{p = 0.017}$			$t_{(15)} = 2.801$ $\boldsymbol{p = 0.013}$		
dPMC RIGHT					$t_{(15)} = 2.820$ $\boldsymbol{p = 0.013}$	$t_{(15)} = 2.158$ $\boldsymbol{p = 0.048}$			
M1 LEFT						$t_{(15)} = 1.632$ $p = 0.123$			$t_{(15)} = 0.245$ $p = 0.809$
M1 RIGHT							$t_{(15)} = -1.471$ $p = 0.162$	$t_{(15)} = 1.321$ $p = 0.206$	

AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex. Table has to be read as follows: cells on top of the columns are the 'input' region and rows represent the 'target.' Bold values in the table indicate significant results.

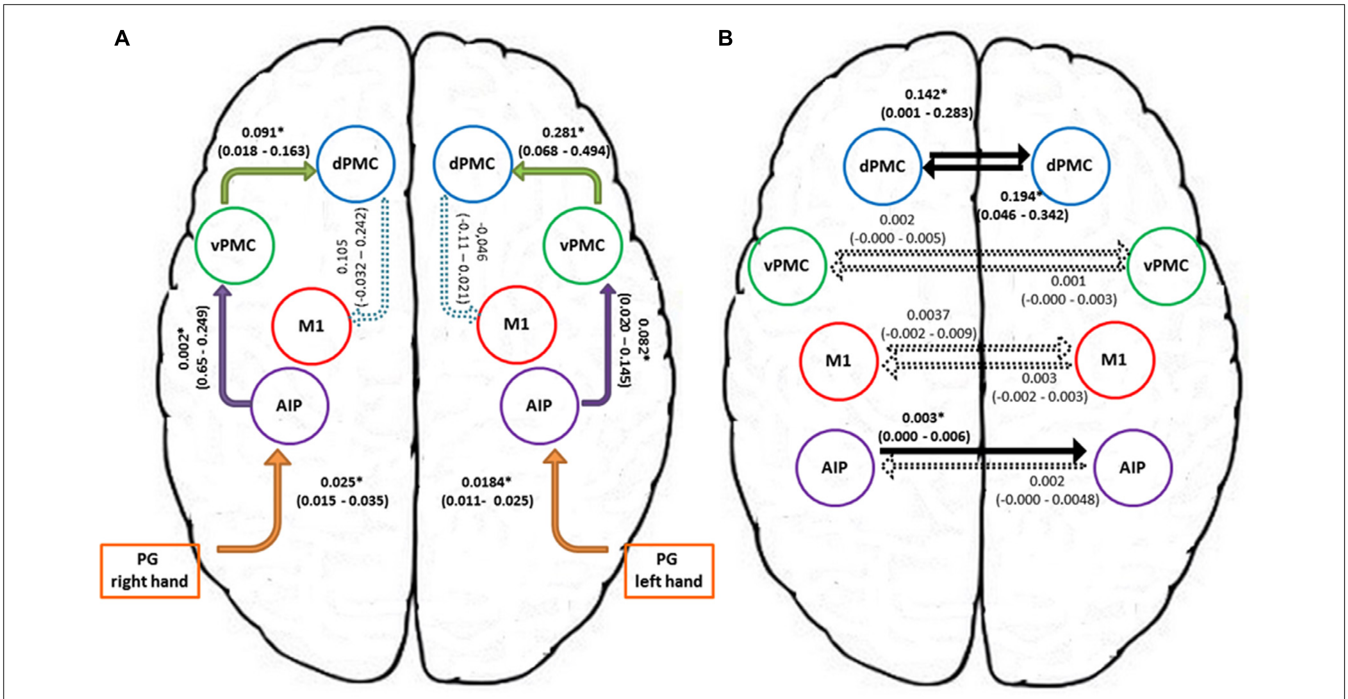

FIGURE 4 | Connection strengths of the tested models. (A) Shows intra-hemispheric connections and **(B)** shows inter-hemispheric connections. Solid lines indicate significant modulation effects. Group-level averages of MAP estimates and 95% confidence intervals are illustrated. The averages were tested against 0 and significant results are signified with $*$ if $p < 0.05$. AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex; PG, precision grip.

Table 4A | Results obtained by paired *t*-test performed on the parameter estimates related to LEFT → RIGHT connections strengths of the winning family LNH ($p < 0.05$).

	AIP_LEFT ↓ AIP_RIGHT (0.0035)	vPMC_LEFT ↓ vPMC_RIGHT (0.0026)	dPMC_LEFT ↓ dPMC_RIGHT (0.142)	M1_LEFT ↓ M1_RIGHT (0.0037)
AIP_LEFT ↓ AIP_RIGHT (0.0035)		$t(15) = -0.695$ $p = 0.498$	$t(15) = -2.119$ $p = 0.051$	$t(15) = -0.067$ $p = 0.948$
vPMC_LEFT ↓ vPMC_RIGHT (0.0026)			$t(15) = -2.116$ $p = 0.051$	$t(15) = -0.067$ $p = 0.948$
dPMC_LEFT ↓ dPMC_RIGHT (0.142)				$t(15) = -0.067$ $p = 0.948$
M1_LEFT ↓ M1_RIGHT (0.0037)				

AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex. Numbers in title column/row indicate the parameter estimate obtained for that connection.

In terms of effective connectivity, previous results (Grol et al., 2007) showed that there are specific, differential changes in effective connectivity between AIP and VPM during reaching-to-grasp movements. A finding that fits with the general notion that the dorsolateral circuit is concerned with controlling grasping parameters of the prehension movement (Jeannerod et al., 1995). Along these lines, the present study shows that when precision grip movements are performed with the right hand, the connections "AIP-vPMC" and "vPMC-dPMC" within the left hemisphere appeared to be significantly modulated. In a similar vein, the "AIP-vPMC" as well as the "vPMC-dPMC" connections were modulated within the right hemisphere, which is supposed to be primarily involved in the control of precision grip movements performed with the left non-dominant hand.

The revelation of "vPMC-dPMC" connections is particularly important because it confirms a series of neurophysiological studies demonstrating an intra-hemispheric cross-talk between these two areas. An important aspect of the neurons recorded in the dPMC area F2 in macaques, is that they showed very similar properties to those previously described in the vPMC area F5 (Murata et al., 1997; Rizzolatti and Fadiga, 1998). Therefore, it has been advanced that both areas F2 and F5 may collaborate in the control of grasping actions. In this respect, Raos et al. (2004) pose an interesting question. That is, why are two premotor areas involved in grasping actions? In this respect, these authors posited that area F5 is chiefly concerned with the selection of the most appropriate type of grip (Raos et al., 2004). This motor representation is then supplied to area F2 whose neurons presumably keep a memory trace of the selected motor representation as to continuously update hand configuration and orientation while it approaches the object to be grasped.

When looking at inter-hemispheric connections between homologous areas the connection between the right and the left AIPs appears to be significantly modulated for the 'left to right' direction but not viceversa. In both humans and monkeys AIP is a crucial component of the parietal-premotor circuit known to be involved in the 'translation' of object intrinsic properties into specific grips (Rizzolatti and Luppino, 2001). In the present study, we confirm the pattern of a bilateral involvement of AIP, previously found in right-handers using either the right or the left hand (Davare et al., 2007).

However, we further deepen these findings suggesting that there is no bidirectional crosstalk between the two homologous areas, or that such cross-talk could be rather limited to the 'left-right' direction. Indeed, hand shaping during TMS studies appeared to be impaired only when TMS was applied bilaterally to AIP (Davare et al., 2007), while when the AIP virtual lesion was unilateral hand shaping remained intact. The existence of a cross-talk would seem to explain this finding, and both AIPs seemed necessary regardless of the hand being use (Davare et al., 2007). Two further studies

Table 4B | Results obtained by paired *t*-test performed on the parameter estimates related to RIGHT → LEFT connections strenghts of the winning family LNH ($p < 0.05$).

	AIP_RIGHT ↓ AIP_LEFT (0.0021)	vPMC_RIGHT ↓ vPMC_LEFT (0.0018)	dPMC_RIGHT ↓ dPMC_LEFT (0.194)	dPMC_RIGHT ↓ dPMC_LEFT (0.194)
AIP_RIGHT ↓ AIP_LEFT (0.0021)		$t(15) = -0.236$ $p = 0.816$	$\mathbf{t(15) = -2.758}$ $\mathbf{p = 0.015}$	$t(15) = -1.477$ $p = 0.160$
vPMC_RIGHT ↓ vPMC_LEFT (0.0018)			$\mathbf{t(15) = -2.765}$ $\mathbf{p = 0.014}$	$t(15) = -1.202$ $p = 0.248$
dPMC_RIGHT ↓ dPMC_LEFT (0.194)				$\mathbf{t(15) = -2.804}$ $\mathbf{p = 0.013}$
M1_RIGHT ↓ M1_LEFT (0.0003)				

AIP, anterior intraparietal; vPMC, ventral premotor cortex; dPMC, dorsal premotor cortex; M1, primary motor cortex. Bold values in the table indicate significant results.

demonstrated that unilateral AIP lesions are unable to alter the ability to shape the hand as to grasp the object hand conformation except when object size and orientation are modified unexpectedly (Tunik et al., 2005; Rice et al., 2006).

As these findings concern grasping execution, they support the hypothesis that a bilateral AIP involvement is required for precision grip movements and that this aspect is a distinctive feature of the anterior sector of the posterior parietal cortex (for review see Castiello, 2005; Culham et al., 2006; Castiello and Begliomini, 2008; Filimon, 2010). Noticeably, in the present study the pattern of connectivity found within this area has a specific direction depending on the hand used. In particular, an increase in connectivity appears to be evident when right-handers use the left hand and, therefore, the right hemisphere is chiefly involved. In fact, inter-hemispheric connections between homologous areas appear to be boosted mainly for the right-left direction when the LNH is used, as if the accomplishment of a precision grip movement with the LNH would require additional processing coming from the left, dominant hemisphere. The superiority of the right hand in high precision inter-joint coordination and in performing dexterous finger movements and trajectory formation has been observed in right-handers (Healey et al., 1986). The accuracy required by the task described in the study presented here and the evident need to determine precise contact points both point to right hand superiority in right-handers, suggesting that when the precision grip movement is performed by the RDH, the left AIP is able to accomplish the sophisticated visuomotor transformation underlying this movement without 'contributions' coming from its homologous in the right hemisphere.

In contrast to the AIP, the connection amongst the right and left dPMC appears to be modulated in both directions. More specifically, as outlined by the BMA results, the modulation of the connections from the left to the right dPMC almost reached significance. In contrast the remaining 'left to right' connections were far from being significant (see **Table 4A**). When looking at the 'right–left' (**Table 4B**) connections, the modulation effect exhibited by the connections between the dPMC appears to be stronger in comparison with all the other inter-hemispheric connections, suggesting that the modulation effect induced by a precision grip movement performed with the LNH is maximally expressed in terms of on-line monitoring 'contribution,' accomplished by the dPMC (Davare et al., 2006; Begliomini et al., 2008).

To summarize, when comparing the strength of interhemispheric connections it is evident that for the 'left to right' direction there are no differences. However, when comparing 'right to left' interhemispheric connections, the connection between the right and left dPMC is much stronger than the connection between the AIP, vPMC, and M1 and their homologous in the left hemisphere. This might indicate that when the precision grip movements is performed with the LNH the ipsilateral dPMC is recruited to a higher extent. In other words, the right hemisphere is in charge of the planning and the execution of the performed action, but is also recruiting the left dPMC to perform the action successfully. It seems, therefore than when a precision grip is performed with the LNH a 'bridge' across hemispheres at the level of the dPMC is activated. In other words, the hemisphere devoted to manage the ongoing action recruits resources also from the other hemisphere. Support to this contention comes from previous neuroimaging evidence suggesting that during the performance of grasping movements with the left hand only the dPMC within the right hemisphere appears to be significantly activated (Begliomini et al., 2008).

These neurophysiological and neuroimaging findings demonstrating the key role of dPMC in controlling distal actions (Raos et al., 2003, 2004) may provide an explanation for these effects and compelling evidence that there are neurons in the distal forelimb representation within area F2 that are specifically selective for the type of prehension required to grasp an object (Raos et al., 2003). They also underline the relevant role dPMC in the on-line control of goal-related hand movements. The increase in connectivity between the dPMC areas outlined by our studies for the 'left–right' direction could indicate that they are activated differentially as the non-dominant left-hand is less skilled and requires more control to perform the tasks.

To conclude, our results shed new light on the complex intra- and inter-hemispheric interplay that takes place within the cortical motor system underlying grasping actions. The results not only validate neurophysiological and neuroimaging data at the level of the grasping circuit, but also allows examining the organization of areas for grasping movements performed with either the dominant or the non-dominant hand in both hemispheres. In the future a DCM approach may serve to assess and evaluate similar processes in left-handers as to understand whether the neural organization of grasping may change with respect to handedness.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/Journal/10.3389/fpsyg.2015.00167/abstract

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 16 October 2014; accepted: 02 February 2015; published online: 24 February 2015.

Citation: Begliomini C, Sartori L, Miotto D, Stramare R, Motta R and Castiello U (2015) Exploring manual asymmetries during grasping: a dynamic causal modeling approach. Front. Psychol. ***6****:167. doi: 10.3389/fpsyg.2015.00167*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 12 January 2015
doi: 10.3389/fpsyg.2014.01513

Skilled performance tests and their use in diagnosing handedness and footedness at children of lower school age 8–10

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Previous research has shown that hand and foot preferences do not develop in parallel in children and it has been discovered that in children foot preference stabilizes later. Therefore, the aim of this study is to verify whether the differences in stabilization will also be manifested through less consistent results of selected skilled foot performance tests in a comparison with selected skilled hand performance tests. A total of 210 8–10 year old children from elementary schools were recruited for this study. Hand and foot preferences were first tested using hand and foot preference observable measure tasks; consequently, all participants performed four skilled hand performance tests and three foot performance tests. Unlike in complex skilled hand performance tests, which showed a significant convergent validity 0.56–0.89 with hand preference tasks, in complex skilled foot performance tests a very low convergent validity 0.25–0.46 with foot preference tasks was detected. The only skilled foot performance indicator which showed an acceptable convergent validity with foot preference tasks was the "foot tapping" test 0.65–0.85, which represents rather a gross motor activity. Moreover, further results of the tests suggest that complex or fine motor performance tests used for diagnosing laterality of the lower limb that have a manipulative character probably do not represent suitable indicators for children in the given age category. The same trend was revealed in both females and males. This indicates that the level of laterality assessed as difference in skilfulness between the preferred and the non-preferred limb in children in the given age group probably develops in the same way in both genders.

Keywords: handedness, footedness, performance tests, laterality, children, fine motor, gross motor

INTRODUCTION

Numerous studies have in the past been dedicated to human laterality, which represent a multidimensional trait (Corballis, 2010). It is well known, for instance, that in the adult population 90% of people prefer to use their right hand for common manual tasks, whereas about 10% of the population are so called left-handers (Annett, 1994; Raymond et al., 1996; Bryden et al., 1997; McManus, 2002). Another important finding is that throughout human life, the development of laterality is a very active process affected by both genetic and environmental factors (see: Porac et al., 1980; Geschwind and Galaburda, 1987; Halpern and Coren, 1991; Annett, 2002; McManus, 2002).

Research into development of laterality in children has shown that it has different phases with respect to ontogenesis. The authors McManus et al. (1988) suggested that handedness in children is generally defined by one basic factor and begins to become fixed around the age of 3; it becomes stabilized and its level increases between 3 and 7 years of age. According to the authors, stabilization gradually weakens between 7 and 9 years of age (McManus et al., 1988). Studies of Cavill and Bryden (2003) or Whittington and Richards (1987) have proven that the development of handedness (right or left) can be determined in children relatively early; which is not entirely true for strength and consistency of handedness (De Gostini et al., 1992). Development of consistency and the level of preference of upper limbs in children has also been studied by authors using so called reaching tasks (e.g., Bryden and Roy, 2006; Carlier et al., 2006), which focused on whether a child would also manipulate with a tool using the preferred upper limb in the case that the tool was placed counter-laterally to the preferred hand. The conclusions of these studies showed that in this kind of motor activity 6- to 10-year-olds children demonstrate significantly more stable consistency of upper limb preference than younger children (Bryden and Roy, 2006; Carlier et al., 2006). Leconte and Fagard (2004), who also used the reaching task approach, revealed that consistency of handedness in children changes with the complexity of the activity which the child is forced to do with his/her upper limb. The authors also add that development of strength and consistency of handedness in children represents an important dynamic process (Leconte and Fagard, 2004).

In comparison with the number of studies on development of the upper-limb laterality, less research has been done into the development of footedness. Coren et al. (1981) found that 3- to 5-year-olds children, as well as a selected population of high-school students, demonstrated a significant right-hand preference. Their findings at the same time revealed that pre-school children had significantly less distinct lower limb preference (Coren et al., 1981). Studies by Gabbard et al. (1991), Gabbard (1992), and Gentry and Gabbard (1995) also found that foot preference in 3- to 5-year-olds children is much less consistent than hand preference. On average, the agreement of upper and lower limb preference in right-handers was 67% while in left-handers it was only 17%. According to the authors, significant stabilization of lower limb preference happens later, between 8 and 11 years of age (Gabbard, 1992; Gentry and Gabbard, 1995). A review study by Gabbard and Iteya (1996) also revealed that in 3- to 5-year-olds mix-footedness appears with twice as much occurrence as mix-handedness (Gabbard and Iteya, 1996). By contrast, Gudmundsson (1993), who studied conformity between upper and lower limb preference in pre-school and younger school children aged 3–11, found 85 and 87% conformity, respectively (Gudmundsson, 1993).

In the diagnosis of laterality, according to Corballis (2009), for example much less attention is paid to the detailed skilled performance approach (Corballis, 2009). The above-mentioned diagnosis of preference allows only a very limited detailed expression of strength of handedness or footedness. Consequently, in past decades performance tests have been created and verified which primarily focus on the difference between the upper limbs in performing the same motor tests (Scharoun and Bryden, 2014). Research has shown that in both children and adults the different skilfulness in terms of speed, precision or correctness of execution of motor activities strongly corresponds with upper limb preference (Peters, 1976; Annett et al., 1979; Rigal, 1992; Carlier et al., 1993; Cornish and McManus, 1996; Nalcaci et al., 2001). Nevertheless, it has also been found that the level of correspondence between preference and performance depends, to a great extent, on the type of performance test. In this context, Annett (1992) observed that the more the activity is of a fine motor character, the more significant the higher skilfulness of the preferred upper limb (Annett, 1992). The authors Roy et al. (1994) and Sainburg and Kalakanis (2000) later added that this considerably higher skilfulness of the preferred upper limb is observed primarily in motor activities in which higher demands are put on: (1) coordination and (2) integration of more segments of the limb, involved in the activity (e.g., shoulder and elbow joints; Roy et al., 1994; Sainburg and Kalakanis, 2000).

Performance tests to evaluate different skilfulness have also been created for lower limbs (see Knights and Moule, 1967; Beling et al., 1998). However, they showed congruency with the determined foot preference solely in the adult population.

In connection with laterality assessment, Rigal (1992), Steenhuis (1999) and Corey et al. (2001) have suggested that for reliable diagnostics, both preference indicators and performance tests should be used because laterality in humans does not represent a unidimensional trait (Rigal, 1992; Steenhuis, 1999; Corey et al., 2001). Even though previous studies focused on the development of upper and lower limb laterality, they mostly assessed development of handedness and footedness and their stability in the child population. The conclusions of studies focused on the question of consistency of upper and lower limb preference in child population suggest that stabilization of lower limb preference represents in children a longer process than stabilization of hand preference (see Gabbard, 1992; Gentry and Gabbard, 1995; Gabbard and Iteya, 1996). However, in connection with this finding we have observed that there are not enough studies attempting to verify whether later stabilization of the lower limb preference is also manifested in the results of performance tests for lower limbs that are used to diagnose laterality in the child population. The results of our previous research have suggested that primarily complex skilled foot performance tests do not show the differences between the preferred and the non-preferred lower limb with sufficient accuracy in 8- to 10-year-olds. In the monograph Musálek (2013), three identical performance tests (for the lower limb) were modeled using the confirmatory factor analysis for the population of 8- to 10-year-olds and for 17- to 19-year-old adolescents. These were complex motor activities which integrated more systems: (1) moving a small object by the lower limb in a limited space and (2) slalom with a tennis ball between obstacles and (3) an activity which focused primarily on speed while performing a simple task – foot tapping. The revealed results were extremely interesting. While in the adolescent population (17- to 19-year-olds), both complex tests had acceptable factor loadings in range: 0.61–0.72 for the modeled factor "foot performance," in 8- to 10-year-olds factor loadings of the tests significantly lower in a range between 0.38–0.43 with respect to the "foot performance" factor. On the other hand, the foot tapping test showed a strong relationship to the "foot tapping" factor in both children and adolescents with factor loads 0.84 and 0.92, respectively. It was also revealed that loads of both complex skilled foot performance tests used in this study were for both children and adolescent populations significantly lower in comparison with complex fine motor tests for the upper limb ("spiral tracing," "dot-filling"; Musálek, 2013). This result could be found due to the fact that upper limbs are primarily designed for manipulation, whereas lower limbs have primarily a postural function (Woodburne and Burkel, 1994, p. 87; Christou et al., 2003; Palastanga and Soames, 2011, p. 202). Therefore, based on this information we assume that in the given category of 8- to 10-year-olds skilled foot performance tests (spiral tracing by small cube; while standing, slalom with ball between obstacles) will show fewer differences and more inconsistencies (i.e., weaker lateralization) than complex tests designed for the upper limbs.

Moreover, a number of studies have also revealed that significant differences exist between males and females concerning consistency of handedness – it has been revealed that there is a significantly higher number of mixed-handers among males (e.g., Whittington and Richards, 1987; Sommer et al., 2008; Johnston et al., 2009). From the point of view of ontogenesis, a very interesting difference between males and females has been revealed in the strength of neural pathways leading into the cerebellum. These pathways which are involved, among other things, in realization of fine motor skills are according to Gurian et al. (2001) significantly stronger in females. Therefore, the second question studied in this research is whether the level of laterality assessed as difference in skilfulness between the preferred and the non-preferred limb will differ in males and in females. We suppose that such difference might be revealed in the form of a different level of relationship factor loadings – in selected performance tests to modeled factors: (1) hand performance, (2) foot performance.

MATERIALS AND METHODS

PARTICIPANTS

A total of 210 typically developing 8- to 10-year-olds ($n = 107$ males and $n = 103$ females; $M_{age} = 9.1$, SD = ± 0.78) from the Czech Republic were recruited for the current study. All participants were pupils of state primary schools in the capital Prague. The selection of the research file was done using the intentional selection process method. The following criteria for selection of participants were used:

(1) pupils were chosen only from schools which had a similar number of pupils in the given age category,
(2) only schools without any specific specialization (e.g., technical, artistic, sport, or linguistic) were selected,
(3) schools and classes with integrated children with special needs were not included in the selection.

As this study draws on the research (validation of variables for diagnosing of motor manifestations of laterality) performed at these selected schools in 2011 and published in 2013 (Musálek, 2013), all participants were chosen from the same schools, as in the previous research. We decided on this concept of an intentional selection process method in order to ensure maximum homogeneity of the file with respect to the findings of 2011.

The 8–10 age category was selected because at this age children's motor skills are harmoniously developed with stable coordination patterns and this age is called the golden age of skill motor development (Ljach, 2002).

Ethics approval was granted by the Ethics Commission of the Faculty of Physical Education and Sport, Charles University. In addition, parental consent was obtained for all individuals.

APPARATUS

In order to verify whether the selected skill performance tests really detect a difference in performance of the preferred and the non-preferred upper and lower limbs, the results of the seven selected skilled performance tests were first correlated with the results of seven observable preference measure tasks (four for handedness, three for footedness). The indicators used for evaluation of hand preference and foot preference have been validated for the Czech child population aged 8–10. Factor loads of hand preference indicators in a range: $\lambda = 0.85–0.93$, generic reliability McDonald $\omega = 0.95$; factor loads of foot preference indicators in a range: $\lambda = 0.66–0.90$, generic reliability McDonald $\omega = 0.81$ (Musálek, 2013). The results of the preference observable measure tasks also served to determine the preferred and the non-preferred limb as a necessary precondition for the selected skilled performance tests to be carried out in accordance with the given rules. Six of the seven observable preference measure tasks have already been used in previous research where theses indicators were approved as valid and reliable either as questionnaire items or preference tasks (e.g., Annett, 1970; Barnsley and Rabovitch, 1970; Oldfield, 1971; Sharman and Kulhavy, 1976; Tapley and Bryden, 1985; Rigal, 1992; Coren, 1993; Bishop et al., 1996; Doyen and Carlier, 2002; Mamolo et al., 2006).

At the same time, all seven performance tests were validated for the Czech child population aged 8–10 years. Five of them – four for handedness: (1) spiral tracing, (2) dot-filling, (3) tweezers and beads, (4) twisting box; and one for footedness: foot tapping – had an acceptable level of factor validity with respect to the modeled factors: (1) hand performance $\lambda = 0.58–0.82$. and (2) foot performance $\lambda = 0.92$. Subsequently approximated generic reliability of the tests modeled only under one factor "Performance of locomotive organs" had value McDonald $\omega = 0.83$. These five tests have already been replicated in the study Scharoun et al. (2013) for the assessment of different performance of the preferred and the non-preferred upper and lower limbs in children with ADHD and their neurotypical controls. The results of this study revealed that all five performance tests are sufficiently sensitive to determine the performance of the preferred and the non-preferred limb and to detect motor problems in children with ADHD (Scharoun et al., 2013).

Preference strength was determined based on laterality quotient calculation, for which equations from previous studies were used (e.g., Humphrey, 1951; Harris, 1958; Bryden et al., 2007; Kalaycioğlu et al., 2008). Each execution in preferential tasks was marked 1 when right limb was used and 0 when the left limb was used.

Laterality quotient for the upper and lower limbs was calculated using the formula

$$LQ = \frac{R - L}{R + L} * 100$$

Hand preference

Throwing on target. The aim of the participant who sits on chair was to throw the foam ball with 58 mm in diameter using one hand to the target which was placed 2 m from participant. Task was repeated three times.

Ring by bell. The examiner places a (metal) bell on the desk in front of the participant so that there was the same distance to both his/her hands. The aim of the participant was to take the bell in one hand and ring it.

Card reaching task (Bishop task). This task included A3 sheet of paper, divided in half by a vertical line The paper contains seven rectangular boxes with the dimensions of 6 cm × 3 cm forming a semicircle. There were seven cards in total in the boxes on the paper, each card having a different, clearly distinguishable color. Each box had its own description: the first box on the left was marked –3 on the shorter side, the second on the left was marked –2, etc., and the last box on the right was marked +3. The middle box on the axis of the paper was marked 0. The aim of the participant was to turn the card with the required color using one hand. The examiner first chooses the color of the card that s/he placed in the box marked 0. If the participant turned this card using the right hand, the examiner required him/her to turn the colored cards in the boxes marked in the following order: +2, –2, +3, –3. If the participant turned this card using the left hand, the examiner required him/her to turn the colored cards in the boxes marked in the following order: –2, +2, –3, +3. Examinator recorded frequency of using right hand or left hand, respectively.

Erasing. The examiner places an erasing rubber with the dimensions of 4.5 cm × 2.5 cm on the desk in front of the participant so that both hands of the participant were in the same distance. Then the examiner asked the participant to erase the prepared drawn line.

Foot preference

Kick to the ball on target. The aim of the participant was to kick the foam ball with 58 mm in diameter in order to hit the wooden block with an edge length of 40 mm placed 2 m from the ball. The kick was performed three times. After each attempt the examiner returned the ball to its original position.

Using one foot, tap the rhythm that I am clapping. The participant sit on a chair in free space. The examiner claps a simple rhythm with a maximum of five claps. The task of the participant was to tap this rhythm on the floor using one lower limb.

Perform jumps forward using one leg. The task of the participant was to perform jumps forward on one leg from examiner to definite point. It was done twice by participant.

Skilled hand performance tests

Spiral tracing. The score sheet contains pre-drawn white spirals of the same shape and length in two gray square boxes with a side length of 50 mm. The largest diameter of the spirals was 41 mm, the thickness (width) of the spiral being 2 mm. The spiral in the right box is intended for the action of the right hand, and the spiral in the left box for the action of the left hand. The aim of the participant was to draw a spiral in the designated area of the spiral-shaped image, from the outer edge to the center. The position of the score sheet hadn't to be changed during the entire test. An error, penalization 2 s, was noted when the participant left the designated area while drawing. This task was completed by non-preferred and preferred hand. The examiner recorded the final time after each drawing.

Dot-filling. There were two boxes with circles on the inside page of the score sheet. The circles in left box are intended for the action of the left hand, and the circles in the right box are intended for the action of the right hand. Each of the boxes contains 90 identical circles. The diameter of a circle is 2 mm. The aim of the participant was to mark dots in the circles, in order to place the dot within the circle in the specified time of 30 s. Only those marks within the circles were counted toward performance. Task was completed by non-preferred and preferred hand.

Moving beads from one box into another using tweezers. This task included two open matchboxes behind each other and a pair of tweezers with a length of 150 mm on the desk in front of the participant so that there is the same distance between both his/her hands and the closer matchbox; the closer matchbox contains 20 beads with 5 mm in diameter, and the second is empty. The aim of the participant was to move the beads one by one from the full box to the empty box using the tweezers in the specified time of 30 s. The task was completed with the preferred and non-preferred hand, where the number of beads transported in 30 s was recorded.

Turning a box alternately with the front and the rear side on the table. This task included a closed empty matchbox with the front facing upward in front of the participant at the midline. The aim of the participant was to turn the matchbox using one hand by its front and back alternately faces the desk. The matchbox had to always touch the desk with one of its parts, i.e., the matchbox hadn't to be lifted from the desk. The task was completed with the preferred and non-preferred hand, where the number of turns in 30 s was recorded.

Skilled foot performance tests

Foot tapping. For this task, the participant stood next to a desk, with the preferred leg closest to the desk The aim of the participant was to perform tapping in a standing position for 30 s using a lower limb so that the motion is performed in the sagittal plane. The participant taught the ground in front of him/her with the heel and the ground behind him/her with the tip, the range of the motion being the length of one foot of the participant. The task was completed with the preferred and non-preferred foot, where the number of tapps in 30 s was recorded (Musálek, 2013).

Unlike the "foot tapping" test, the following two tests (slalom with a ball between obstacles and spiral tracing by small cube) proved valid for adolescent population of selected students from the Czech Republic; however, this is not true for children aged 8–10 (Musálek, 2013). Also due to the previous equivocal results, we used the following skilled foot performance tests in this study: (1) slalom with a ball between obstacles and (2) spiral tracing by small cube; this test was derived from two tests – spiral tracing test used for hand and moving a cube in the "maze" while standing performed by foot. Both tests underwent multiple content validation with instructions and technical parts (tools) adapted so that different performance of the preferred and the non-preferred lower limb could be assessed.

The content validity of both tests was assessed by six selected experts in: anthropology, kinesiology, psychology, motor development, special pedagogy, and neurology.

While standing, slalom with ball between obstacles. This task included eight cubes on the floor in the line. Distance between each two cubes was 10 cm. In distance 15 cm in front of first cube and 15 cm behind last cube was on the floor attached color line. The aim of the participant was to performed slalom with tennis ball with 65 mm in diameter between cubes. Participant could move ball between obstacles only from top. Each contact of the ball and obstacle is error. This error was counted as 2 s penalty. Participant had to go through whole track from line to line. The task was completed with the preferred and non-preferred foot.

Spiral tracing by small cube. This task included A3 sheet of paper which had a spiral drawn on both sides on the floor. The spiral on each side of the paper was 30 cm in diameter with the thickness (width) of the spiral being 4 cm. The aim of the participant was to use the cube provided with a width of 1.5 cm to copy the spiral path in the designated area of the spiral-shaped image, from the outer edge to the center. The spiral had to be copied only by moving the cube by imposing pressure on the side of the cube; it was therefore forbidden to manipulate the cube by placing the sole of the foot on the top of it. An error, penalization 2 s, was noted when the participant left the designated area while copying. This task is completed by non-preferred and preferred foot. This motor test was carried out without preparation. The examiner recorded the final time after each copying.

STATISTICAL ANALYSIS

In order to determine the level of the relationship between the selected preference measure observable tasks and skilled performance tests, biserial and polyserial correlations were used. Consequently, difference in performance of the preferred and the non-preferred limb for each skilled performance indicator were assessed by a paired t-test with the level of statistical significance $p < 0.05$ and substantive significance Cohen $d > 0.7$ (Cohen, 1988). In order to determine possible differences in the structure of hand and foot performance in females and males, the confirmatory factor analysis multigroup modeling approach was used (Muthén and Muthén, 2010). Robust maximum likelihood (Ferron and Hess, 2007; Muthén and Muthén, 2010) was used as the estimate parameter because in our case the multivariate normality of data condition was not fulfilled. The data analysis was done using the statistical software M-Plus 6 (Muthén and Muthén, 2010) and NCSS2007 (Hintze, 2007).

RESULTS

First we analyzed the number and ratio of those that were pronounced: right-sided children, left-sided children and children who at least once changed limbs while performing the preference tasks (see Methods apparatus). Of the 210 participants, 136 children had uncrossed lateral preferences (right-handed and right-footed), (65 males and 71 females) LQ = 100, and 18 children had uncrossed lateral preferences (left-handed and left-footed), (10 males and 8 females) LQ = 0. The LQ of the remaining 56 children (32 males and 24 females) ranged within LQ = 31.25–75.

The subsequent correlation analysis between preference observable measure and skilled hand performance tests is shown in **Table 1**. The tests which detect different skilfulness of the preferred and the non-preferred upper limb manifest sufficient convergent validity with hand preference observable measure: correlation in a range $r = 0.56$–0.89. It follows that the selected hand performance tests have a sufficient capacity to adequately determine the difference between the preferred and the non-preferred upper limb.

On the other hand, **Table 2**, shows that the correlation analysis between foot preference observable measure and skilled foot performance tests revealed that two of three performance tests (slalom between obstacles and spiral tracing with small cube) do not manifest a satisfactory convergent validity $r = 0.25$–0.46 with foot preference observable measure. This finding suggests that fine motor or complex tests for lower limbs lack sufficient sensitivity to distinguish between the preferred and the non-preferred lower limb in the given age group.

Table 1 | Convergent validity between hand preference observable measure and hand performance tests.

Item	Throwing	Ring the bell	Bishop task	Erasing
Spiral tracing	−0.89	−0.84	−0.66	−0.82
Dot-filling	0.70	0.66	0.64	0.63
Twistbox	0.78	0.75	0.64	0.66
Tweezers and beads	0.75	0.70	0.58	0.56

Table 2 | Convergent validity between foot preference tasks and foot performance tests.

Item	Kicking	Tapp rhytmus	Hop forward
Slalom with ball between obstacles	**−0.46**	**−0.33**	**−0.26**
Spiral tracing by small cube	**−0.39**	**−0.43**	**−0.25**
Foot tapping	0.85	0.74	0.65

Correlations lower than 0.50 are shown in boldface.

Next we assessed the capacity of the seven skilled performance tests to determine preferred and non-preferred upper and lower limb by significance of difference in skilfulness of the preferred and the non-preferred limb.

Table 3 shows that all the skilled hand performance tests used were able to significantly determine the difference between skilfulness of the preferred and the non-preferred upper limb, with the preferred upper limb being significantly more precise and quicker $p < 0.05$, *Cohen d* in the tests $d = 0.84$–2.91. On the contrary, the same cannot be said about the results of the foot performance tests. Among them, only the "tapping" test showed significant capacity to determine the difference in skilfulness of the preferred and the non-preferred lower limb $p < 0.05$ and *Cohen d*, $d = 1.22$. The other two tests, which were of a complex motor character, with the "slalom with a ball between obstacles" test having extra demands on balance, did not confirm the significance of the different performance of the preferred and the non-preferred lower limb *Cohen d* ranging within $d = 0.22$–0.27. These results together with findings regarding convergent validity for the lower limb (see **Table 2**) support the hypothesis that fine motor or complex tests for diagnosing lower limb laterality in children of the given age category are not suitable due to their low discrimination capacity between the preferred and the non-preferred lower limb.

Next, we modeled all skilled performance tests in two-factor structure in order to determine whether the relationship between the individual indicators and defined latent variables upper limb performance and lower limb performance do not differ significantly in females and males.

The multigroup model assessed whether the child's gender in the given age group does not represent a significant factor in the process of lateralization. A two-factor model for females and males shows that factor load does not differ significantly for most items. **Table 4** also shows that most indicators detected laterality (differences in skilfulness of the preferred and the non-preferred limb) between males and females aged 8–10 with approximately the same strength. The "foot tapping" performance test was the only exception, revealing significant difference between factor load in males, $r = 0.56$, and females, $r = 0.74$ at the significance level of $p < 0.05$. There could be two reasons for this result. Firstly, possibly in males stabilization of lower limb performance takes

Table 3 | Differences in performances between preferred and non-preferred hand in skilled hand performance tests.

Item	M NP – limb	SD NP – limb	M P – limb	SD P – limb
Hand performance tests				
Spiral tracing	79.3 s	23.4	44.2* s	13.8
Dot-filling	12.2 dots	5.1	34.3* dots	8.3
Tweezers and beads	7.9 beads	1.7	12.1* beads	2.1
Twistbox	38.4 twists	4.9	43.3* twists	5.1
Foot performance tests				
Slalom with ball between obstacles	53.7 s	17.8	50.9 s	16.6
Spiral tracing by small cube	43.7 s	16.4	42.1 s	15.8
Tapping foot	32.4 tapps	7.1	41.2* tapps	7.3

*NP – limb, non-preferred limb; P – limb, preferred limb; *significant difference between performance of non-preferred and preferred limb p < 0.05.*

Table 4 | Factor loadings of the 2-factor model – factors: (1) upper limb performance and (2) lower limb performance.

Factors and used performance tests	Male		Female	
	λ	Uniq	λ	Uniq
Upper limb performance factor				
Spiral tracing	−0.84	0.25	−0.78	0.43
Dot-filling	0.78	0.39	0.87	0.24
Twistbox	0.63	0.56	0.67	0.55
Tweezers and beads	0.47	0.76	0.58	0.67
Lower limb performance factor				
Slalom with ball between obstacles	−0.32	0.86	−0.38	0.74
Spiral tracing by small cube	−0.30	0.89	−0.26	0.92
Tapping foot	0.56*	0.69	0.74*	0.44

*Names of factors are in boldface; λ, factor loading; Uniq, uniqueness - residual variance; *significant difference between factor loadings p < 0.05.*

longer. Or secondly, that on the contrary the smaller difference in performance of the right and the left lower limb is caused by the relationship between the character of the test and a certain environmental factor.

DISCUSSION

The aim of the study was to verify in a selected child population whether later stabilization of lower limb preference in comparison to hand preference determined in children (Coren et al., 1981; Gabbard et al., 1991; Gabbard, 1992; Gentry and Gabbard, 1995) is also manifested in lower consistency of performance test results for lower limbs used for the diagnosis of laterality. Within this question we have further studied whether the speed of lateralization diagnosed by selected indicators differs with respect to gender.

First, diagnosis of upper and lower limb preference was carried out using validated measure observable tasks.

Polyserial correlation between all selected skilled hand performance tests and hand measure observable task clearly demonstrated significant convergent validity ranging within $r = 0.56$–0.89. On the other hand, very weak correlations with foot preference ranging within $r = 0.25$–0.46 were determined in polyserial correlation between foot preference tasks and skilled foot performance tests in "slalom between obstacles" and "spiral tracing with small cube" tests. Consequently, convergence was not confirmed for two-foot performance tests and preference tasks, which suggests that lower limb lateralization in children is probably not identical in strength with upper limb lateralization. t-test results showed that selected indicators, which have also been validated for the Czech population, assessing upper limb preference in 8- to 10-year olds determine the difference between the preferred and the non-preferred upper limb $p < 0.05$ very well, with the non-preferred upper limb always being slower and less precise. This is in line with the conclusions of studies demonstrating that different skilfulness in speed, precision and correctness of execution of the motor activity strongly corresponds with the preferred upper limb in children (i.e., Annett et al., 1979; Rigal, 1992; Carlier et al., 1993; Cornish and McManus, 1996; Nalcaci et al., 2001). Moreover, these results also correspond with the conclusions of studies (Whittington and Richards, 1987; McManus et al., 1988; Cavill and Bryden, 2003; Bryden and Roy, 2006; Carlier et al., 2006) which show that between 6 and 10 years of age stability of hand preference in children is quite firm. In this respect it was also proved that the finer the motor activity, the bigger the differences between the performance of the preferred and the non-preferred upper limb, which confirms the arguments of Annett (1992). The biggest differences between performance of the preferred and the non-preferred upper limbs were found in complex tests with high demands on coordination ("spiral tracing" and "dot-filling"). This supports hypotheses made by Roy et al. (1994) and Sainburg and Kalakanis (2000) or Scharoun et al. (2013). They claim that significantly higher skilfulness of the preferred upper limb is observed in activities in which more segments of the given limb (e.g., shoulder and elbow joint) are involved at the same time (Roy et al., 1994; Sainburg and Kalakanis, 2000; Scharoun et al., 2013).

However, the results of the performance tests selected for the lower limb did not clearly detect a difference in skilfulness of the preferred and the non-preferred lower limb and thus confirmed problems detected with convergent validity in some skilled foot performance tests. Two out of three tests used ("slalom between obstacles" and "spiral tracing with small cube"), which compared to the tapping test by lower limb are more complex and have a finer motor character, revealed insignificant differences in performance between the preferred and the non-preferred lower limb. It is interesting to note that the "slalom between obstacles test" is validized in the CR for the adult population, in which no problems appeared in detecting difference in performance of the preferred and non-preferred lower limb. These findings are in conformity with studies (Knights and Moule, 1967; Beling et al., 1998) which revealed agreement of results of performance tests with determined foot preference solely in the child population. The revealed low sensitivity of complex and fine motor laterality performance tests for lower limb in children could be related to the detected longer stabilization process of the lower limb preference (Coren et al., 1981; Gabbard et al., 1991; Gabbard, 1992; Gentry and Gabbard, 1995; Gabbard and Iteya, 1996). This shows that lower limb performance in children is limitary. Paradoxically, too fine motor tests or too complex tests with high demands on coordination cannot determine the difference between the preferred and the non-preferred lower limb based on the results. Finally, we verified whether the lateralization process of the upper and lower limbs assessed by performance tests happens differently for females and males at this age. A two-factor model where all seven skilled performance tests were tested showed that the sensitivity of the selected indicators for detecting laterality of the upper and lower limbs is quite similar for both genders. This means that the lateralization process for the upper and lower limbs is probably quite similar in females and males at this age. The only difference of some significance revealed was related to factor load of the "foot tapping" test in females $r = 0.74$ and males $r = 0.56$ with factor validity coefficient for females being significantly $p < 0.05$ higher in comparison with factor validity of this indicator in males. This difference might be explained by some environmental factors, in males primarily by collective sports where both lower limbs are used (e.g., football). Consequently, the "foot tapping" test might not be sensitive enough to determine the difference between the preferred and the non-preferred lower limb in males. On the other hand, in females, who are not affected by these environmental factors, or are affected to a much smaller extent, the "foot tapping" test determined the difference between the preferred and the non-preferred lower limbs very well.

CONCLUSION

It was revealed that in skilled hand performance tests, the more complex and more demanding in terms of coordination the motor activity is, the bigger the differences there are between the preferred and the non-preferred upper limb. However, the same result was not proved in skilled foot performance tests. On the contrary, the more demanding the lower limb tests were, the worse the convergence validity of these tests in connection to preference tasks. This finding in children could be related to a longer stabilization process of the lower limb preference (see Coren et al., 1981; Gabbard et al., 1991; Gabbard, 1992; Gentry and Gabbard, 1995). It is interesting to note that the lateralization process assessed by difference in performance in skilled performance tests happens in parallel in both genders.

ACKNOWLEDGMENT

This work was supported by project PRVOUK39, Social-Sciences Aspects of Human Movement Studies.

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Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 30 September 2014; accepted: 08 December 2014; published online: 12 January 2015.

Citation: Musalek M (2015) Skilled performance tests and their use in diagnosing handedness and footedness at children of lower school age 8–10. Front. Psychol. ***5****:1513. doi: 10.3389/fpsyg.2014.01513*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 03 February 2015
doi: 10.3389/fpsyg.2015.00017

Is strength of handedness reliable over repeated testing? An examination of typical development and autism spectrum disorder

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Despite a lack of agreement concerning the age at which adult-like patterns of handedness emerge, it is generally understood that hand preference presents early in life and development is variable. Young children (ages 3–5 years) are described as having weak hand preference; however, older children (ages 7–10 years) display stronger patterns. Here, strength of hand preference refers to reliable use of the preferred hand. In comparison to their typically developing (TD) peers, individuals with autism spectrum disorder (ASD) are described as having a weak hand preference. This study aimed to extend the literature to assess three measures of handedness (Waterloo Handedness Questionnaire – WHQ, Annett pegboard – AP, and WatHand Cabinet Test – WHCT) in two repeated sessions. The first research question aimed to delineate if the strength of hand use changes across testing sessions as a function of age in typical development. Right-handed children reported a reliable preference for the right hand on the WHQ, similar to adults. A marginally significant difference was revealed between 3- to 4- and 5- to 6-year-olds on the AP. This was attributed to weak lateralization in 3- to 4-year-olds, where the establishment of hand preference by age 6 leads to superior performance with the preferred hand in 5- to 6-year-olds. Finally, for the WHCT, 3- to 4-year-olds had the highest bimanual score, indicating use of the same hand to lift the cabinet door and retrieve an object. It is likely that the task was not motorically complex enough to drive preferred hand selection for older participants. The second research question sought to determine if there is difference between (TD) children and children with ASD. No differences were revealed; however, children with ASD did display variable AP performance, providing partial support for previous literature. Findings will be discussed in light of relevant literature.

Keywords: handedness, hand preference, hand performance, children, autism spectrum disorder (ASD)

INTRODUCTION

Handedness is a multidimensional motor function which identifies the hand one prefers to use for a variety of unimanual tasks (i.e., *preference*) and the ability to perform more effectively with one hand (i.e., *performance*; Corey et al., 2001). Such dimensions enable handedness to be quantified according to *direction* and *degree*. Direction identifies whether an individual is left- or right-handed; whereas degree quantifies how strongly a person prefers one hand in comparison to the other both within a task and across time (Steenhuis and Bryden, 1989). A person with a strong hand preference reliably uses their preferred hand. A person with weak hand preference will typically use their preferred hand; however, they may switch to the non-preferred on occasion, thus displaying evident variability in hand selection. Finally a person with mixed or ambidextrous hand preference varies selection equally between both hands. Many studies have reported that approximately 90% of the human population is right handed. The proportion of right and left handers has remained reliable for approximately 5000 years (Coren and Porac, 1977). It is generally understood that left handers display less functional asymmetry than right handers (e.g., Springer and Deutsch, 1998; Yahagi and Kasai, 1999) and thus display an overall weak hand preference.

It has been suggested that preference for one hand emerges very early in life. Early lateralized motor behaviors (e.g., thumb sucking; Hepper et al., 1991), infant postural preferences (Coryell and Michel, 1978) and reaching, and grasping patterns (Marschik et al., 2008) are all thought to contribute to the development of handedness. From 6-months onward a preference for one hand can be detected (see Butterworth and Hopkins, 1993 for a review); however, hand use preference is both variable and malleable (Corbetta et al., 2006), such that different patterns of development are observed.

From early childhood to adolescence (i.e., 3- to 12-year-olds), consensus has not yet been reached regarding the age at which adult-like handedness is attained. It has been suggested that direction of preference is established at the age of 3. In comparison, degree increases between the ages of 3–7 years and more gradually until age 9 (Archer et al., 1988; Longoni and Orsini, 1988; McManus et al., 1988). From this, it is understood that assessment of hand preference is not reliable until age 4 (McManus, 2002).

That said, others (e.g., Bryden et al., 2000a) have described that hand preference is not reliable until age 6, as 3- to 4-year-olds display variable patterns of handedness. Differences in developmental milestones of handedness are likely attributed to different ways of quantifying hand preference and performance abilities (see Scharoun and Bryden, 2014 for a review) as numerous tools are currently in use to quantify handedness. The following will speak to the development of handedness as assessed by means of: (1) measures of hand preference; (2) measures of hand performance; and (3) observational-based assessments of hand preference.

MEASURES OF HAND PREFERENCE

Questionnaires are commonly used to identify the preferred hand for completing an activity (McManus and Bryden, 1992). These measures are based on a continuum from extreme left to extreme right, thus enabling quantification of both direction and, in some cases, degree (Steenhuis and Bryden, 1989) of hand preference. The Waterloo Handedness Questionnaire (WHQ) was used in the current investigation; however, this is one of numerous questionnaires in use. Although such questionnaires are not specifically designed for children, use is prevalent in the literature. For example, in the largest study to date, Carrothers (1947) had classroom teachers report on the handedness of 225,000 school children (grades 1–12) in Michigan. A general pattern of decline in left hand preference (i.e., an increase in right hand preference) was reported with age (Carrothers, 1947). Porac et al. (1980) also noted that the number of right handers increases with age. Two developmental hypotheses were presented to explain such trends: (1) environmental pressures toward right-handedness; and (2) neural development continuing into the third decade of life.

Previous research has also successfully utilized oral administration of questions as alterations to the administration of handedness questionnaires for children as young as 2 (Karapetsas and Vlachos, 1997; Cavill and Bryden, 2003). For example, Cavill and Bryden (2003) used the revised WHQ (20-item) to assess handedness in 2- to 24-year-olds. All age groups appeared right-handed and the distribution of hand preference did not change with age (Cavill and Bryden, 2003). Research to date thus outlines that right handers report a strong preference for the right hand over the course of development. In contrast, left handers display weak preference for the left hand which increases with age, albeit never reaching the degree of strength observed in right handers (e.g., Bryden et al., 2000b; Cavill and Bryden, 2003). Summarizing then, direction of hand preference appears to emerge at a relatively young age (Longoni and Orsini, 1988; McManus et al., 1988), whereas degree undergoes refinement with age.

MEASURES OF HAND PERFORMANCE

Despite successful use of questionnaires with children, considering the subjective nature of their design, hand preference measures possess inherent limitations, and are not particularly reliable for use with children (Bryden et al., 2007). Finally, the large verbal and memory component limits use with children, especially those with developmental disabilities. Performance measures have thus been implemented to differentiate between right and left hand abilities on a particular task (McManus and Bryden, 1992). These measures include, but are not limited to, dot-filling tasks (Tapley and Bryden, 1985), peg-moving tasks (Matthews and Klove, 1964; Annett, 1970b), and manual aiming tasks (Roy and Elliott, 1989).

The current study used the Annett pegboard (AP), long established as a valid and reliable measure of hand performance, which times the movement of 10 doweling pegs (Annett, 1970b). Previous research with this method has revealed peg-moving time decreases with age (Kilshaw and Annett, 1983; Curt et al., 1992; Singh et al., 2001; Annett, 2002; Dellatolas et al., 2003). More specifically, between the ages of 3 and 6, a decrease in movement time by approximately 40% has been reported, alongside a decrease in variability of performance with age (Annett, 2002; Dellatolas et al., 2003). Some researchers have noted no change with age in the performance difference between the two hands (Kilshaw and Annett, 1983; Curt et al., 1992; Annett, 2002; Dellatolas et al., 2003), whereas others describe large performance differences in young children, which decrease with age (Roy et al., 2003; Bryden and Roy, 2005; Bryden et al., 2007). Performance differences have often been attributed to the development of the corpus callosum (e.g., Driesen and Raz, 1995).

OBSERVATIONAL-BASED ASSESSMENTS OF HAND PREFERENCE

The inability to replicate findings in the literature highlight that despite the benefits of performance measures, similar to questionnaires, such measures possess their own limitations. To further elucidate the development of handedness observational-based have been implemented to assess children in a more natural environment (e.g., Kastner-Koller et al., 2007). For example, researchers have overcome these obstacles by means of asking children to perform each item listed on handedness questionnaires. Kilshaw and Annett (1983) observed the hand selected for the 12-item Annett (1970a) Handedness Questionnaire. Similar to other reports, no differences among the age groups were reported; however, younger children displayed weak hand use preferences, characterized by increased variability (i.e., switched between right- and left-hand) compared to older children (Kilshaw and Annett, 1983).

The WatHand Cabinet Test (WHCT; Bryden et al., 2000a), which was used in the current investigation, is another form of observational-based assessment of hand preference. This task enables a skilled score, consistency score, bimanual score, and total score to be computed. Due to minimum verbal requirements, the WHCT has been documented as an accurate means of assessing hand preference, in comparison to questionnaires (e.g., WHQ) and performance (e.g., peg-moving) measures. Bryden et al. (2007) have suggested it is an excellent tool for use with special populations.

Research with the WHCT has revealed young typically developing (TD) children (3- to 4-year-olds) are the least lateralized in comparison to older children and young adults, thus displaying weak hand preference tendencies. Furthermore, research with the WHCT has noted that hand preference is typically established at age 6 and the strength of preference increases with age. With age and maturation, older children (7- to 10-year-olds) display stronger, and therefore more reliable patterns of handedness. That said, Left handers generally display weak hand preference over the course of development, such that some young lefties use their non-preferred hand at least half of the time (Bryden et al., 2000b). All of that in consideration, the test–retest reliability of the WHCT has yet to be established; therefore, one aim of this study was to assess if strength of handedness changes over repeated testing sessions as a function of age.

HAND PREFERENCE IN AUTISM SPECTRUM DISORDER

In comparison to their TD peers, an increased prevalence of left handedness has been reported in individuals with developmental disorders. Impaired left hemisphere functions causing a shift of localization to the right-hemisphere has been proposed (e.g., Geschwind and Behan, 1982). Autism spectrum disorder (ASD) is the most common form of severe developmental disability of childhood. Neural deficits are stereotypical of left hemisphere functions (i.e., language and comprehension skills) and the link between non-right handedness, left hemisphere dysfunction and ASD has become prevalent in the literature (Colby and Parkison, 1977; McCann, 1981; Gillberg, 1983; Neils and Aram, 1986; Soper et al., 1986; McManus and Bryden, 1992; Cornish and McManus, 1996).

Previous work with children with ASD has documented an obvious dissociation between hand preference and performance (McManus et al., 1992) as a result of patterns of lateralization that differ from TD children. For example, children with ASD performed better on the AP with the non-preferred hand, in comparison to the control, who displayed superior performance with the preferred hand (McManus et al., 1992). That said, Cornish and McManus (1996) have reported a decrease in left hand preference from 33% in younger children with ASD (ages 4–5) to 15% in older (ages 12–13) children with ASD. However, strength of preference was never fully comparable to TD children in their study. Cornish and McManus (1996) thus proposed children with ASD have a characteristic and individual pattern of handedness, described as non-right handedness. This idea has been repeatedly confirmed (Hauck and Dewey, 2001; Dane and Balci, 2007) using various preference, performance, and observational measures discussed previously. For example, Markoulakis et al. (2012) confirmed a greater proportion of left handers according to the WHCT, which contrasted self-declared hand preference. That said, reference to non-right-handedness in children with ASD typically refers to performance within a set of trials conducted in a single session. As such, this study aimed to extend the previous literature, by means of assessing handedness over repeated testing sessions in order to delineate if variability in strength of handedness is further exaggerated across time.

Overall, it is clear that young, TD children (3- to 5-year-olds) have weak hand preference tendencies, characterized by test–retest variability. With age and maturation, older TD children (7- to 10-year-olds) display an increase in strength of handedness. In other words, demonstrate more reliable use of the preferred hand. In comparison to their TD peers, children with ASD are described as having an increased frequency of non-right handedness. More specifically, increased rates of ambiguous and mixed-handedness have been documented. This study consists of an extension of previous work, as handedness was assessed in two repeated testing sessions to assess if hand preference tendencies, and performance differences between the two hands vary over time, as a function of age and between TD children and children with ASD.

This study used a cross-sectional approach to assess handedness, by means of preference (i.e., WHQ), performance (i.e., AP), and observational-based (i.e., WHCT) measures. Three different tools were implemented considering several factors may underlie handedness (e.g., Corey et al., 2001). Therefore it is clear to many researchers that a single test is not sufficient as numerous components of hand preference and performance must be considered. As outlined by De Agostini et al. (1992) "*the choice of the items used becomes crucial because this final classification is highly dependent on item choice. . .it should be stressed that the very young child may indeed manipulate an object with both hands not so much because his handedness is not yet established but rather because of factors that are independent of handedness*" (p. 54). Three distinct tools that correlate significantly as measures of handedness were thus selected (Bryden et al., 2000b; Brown et al., 2004). The AP was selected as a measure of hand performance. In comparison, the WHQ and WHCT were used to evaluate hand preference; the former through questionnaire and latter through observation. In other words, the WHCT can be considered an observational-based assessment of preference. Questionnaires are the most commonly and traditionally used assessments of hand preference (McManus and Bryden, 1992); however, considering problems with assessment in children, it has been suggested that measuring handedness through observation is an appropriate and effective alternative (e.g., Karapetsas and Vlachos, 1997). Additionally, these two measures of preference were selected, as the test–retest reliability of the WHCT has yet to be established. Thus, it was necessary to establish how reliable the measure was across time in relation to well established measures.

HYPOTHESES

The specific research questions were as follows. First, does strength of handedness change over repeated testing sessions as a function of age? It was hypothesized that strength of handedness would be more reliably assessed over repeated testing sessions as a function of age. In other words, variability in performance would decrease as a function of age, such that younger children would display weak handedness tendencies, whereas older children would display stronger, and thus more reliable handedness tendencies. Secondly, is there a difference in strength of handedness when comparing TD children and children with ASD matched according to sex and comparable in chronological age? It was hypothesized that TD children would display stronger preference tendencies than children with ASD over repeated testing sessions.

MATERIALS AND METHODS

PARTICIPANTS

A cross-sectional approach was used to investigate handedness. Right-handed TD 3- to 12-year-old children (n = 76), a convenience sample, selected because of accessibility and proximity, of graduate, and undergraduate students from the researchers' institution ($n = 18$) and a group of children with ASD ($n = 13$) participated in this study (see **Table 1**). The institution Research Ethics Board approved all recruitment and testing procedures. Informed consent was obtained.

Table 1 | Participant demographics.

Group	*N*	Mean age (SD)	Male	Female
3- to 4-year-olds	11	3.64 (0.50)	5	6
5- to 6- year-olds	14	5.43 (0.51)	6	8
7- to 8-year-olds	21	7.43 (0.51)	10	11
9- to 10-year-olds	12	9.67 (0.49)	3	9
11- to 12-year-olds	18	11.22 (0.43)	8	10
Adults	18	21.44 (0.78)	10	8
Children with autism spectrum disorder (ASD)	13	8.38 (1.98)	8	5

Children with a formal diagnosis of ASD using DMS-IV-TR criteria (American Psychiatric Association, 2000) from a medical doctor were recruited to participate. This study was limited as IQ was not assessed; however, children were identified as high-functioning on the spectrum. After initial recruitment the autism spectrum quotient: children's version (AQ-Child; Auyeung et al., 2008) was used as a means of quantifying autistic traits. A 50-item parent report questionnaire designed for 4- to 11-year-old children, the AQ-Child considers five areas associated with autism and the broader phenotype: social skills, attention switching, attention to detail, communication, and imagination. A four-point Likert scale is used to assess the degree to which parents agree/disagree with statements about their child (0: definitely agree; 1: slightly agree; 2: slightly disagree; and 3: definitely disagree). Items are reverse scored as necessary. Total AQ scores range from 0 (no autistic traits) to 150 (full endorsement on all items). A cut-off score of 76 has high sensitivity (95%) and specificity (95%); therefore, children with scores lower than 76 ($n = 2$) were excluded from analysis.

PROCEDURES AND APPARATUS

Participants were seated at an age-appropriate table as they completed each task. Each participant was first asked which hand was used for writing (coloring for children) to denote self-report hand preference. Three distinct tools that correlate significantly as measures of handedness were used (Bryden et al., 2000b; Brown et al., 2004): (1) The WHQ, (2) The AP, and (3) The WHCT. To assess if reliable hand preference tendencies are displayed over repeated testing sessions, the entire battery of tests was completed on each of two separate days, with a minimum of 48 h between sessions.

Waterloo Handedness Questionnaire (WHQ)

The 32-item version of the questionnaire was used (Steenhuis et al., 1990). Each question permits five responses: "left always," "left usually," "uses both hands equally often," "right usually," and "right always." A laterality quotient is computed by taking the difference between the total number of left and right hand responses [(right hand – left hand)/(right hand + left hand)] and multiplying the result by 100. It is expected, based on self-report hand preference, that left handers have a negative laterality quotient (i.e., left-hand preference) and right handers have a positive laterality quotient (i.e., right-hand preference).

Adult participants completed the questionnaire individually. The questionnaire was administered orally to TD children by reading each item aloud and explaining the item if necessary. It is important to note that previous research has successfully utilized oral administration of questions as alterations to the administration of handedness questionnaires for pre-school children (e.g., Karapetsas and Vlachos, 1997; Cavill and Bryden, 2003). That said, given the large verbal and memory components requirement, combined with the inability to distinguish how familiar children may be with particular tasks (e.g., which hand would you use to put a nut washer on a bolt; with which hand would you hold a needle when sewing?) the WHQ was not completed with 3- to 4-year-olds. In addition, children with ASD were either unable or unwilling to complete the questionnaire orally; therefore parents were asked to complete the questionnaire on behalf of their children on the first day of collection. As data was collected through different means, there was no means of direct comparison between TD children and children with ASD; therefore WHQ data was only used to confirm self-report hand preference.

Annett pegboard

In this task participants were required to pick up 10 doweling pegs, one at a time and place them into the empty holes as quickly as possible. Two trials were completed with the right and left hands. Starting hand was counterbalanced. The time to complete the task (i.e., hand performance) between touching the first peg to releasing the last was recorded using a stop-watch. If pegs were dropped, the trial was repeated. The average of the two trials for each hand was used for the purpose of analysis. Laterality quotients were the computed by taking the difference between left and right hand performance [(left hand − right hand)/(left hand + right hand)] and multiplying the result by 100. The size of the performance difference between the hands is thought to reflect the strength of hand preference (Provins and Magliaro, 1993). It is expected that left handers display negative laterality quotients and right handers display positive laterality quotient.

WatHand Cabinet Test

As outlined by Bryden et al. (2007), the WHCT

> "was a cabinet 15.5″ × 12″ × 24″. The cabinet was divided, in half, into compartments (one in the upper half and one in the lower half of the box). The top compartment was covered by a door that opened with a hand centered on the bottom edge of the door. The bottom compartment was not covered. The cabinet included two cup hooks centered on the left-hand side (while facing the front) of the cabinet, three inches apart, one above the other. A screw was centered on the right-hand side of the box, a Velcro bull's eye target and ball were located on the top at the back of the cabinet, and a small padlock hung from a hook that was centered on the door located at the front of the cabinet" (p. 831).

Bryden et al. (2007) procedures were followed: "lifting the cabinet door a total of four times, using a toy hammer, placing rings on hooks, tossing a ball to a target, opening a lock with a key, using a screwdriver, pushing small buttons on a gadget, picking up a candy dispenser that was behind the cabinet door" (p. 831). For the purpose of analyses, four sub-scores were computed. The *total score* considered performance of all unimanual tasks; whereas the *skilled score* considered seven tasks that required manual dexterity (i.e., use a toy hammer, place a washer on a hook, toss a ball to a target, open a lock with a key, use a screwdriver, push small buttons on a gadget, use a crayon). These scores were calculated with a laterality quotient by taking the difference between the total number of left and right hand responses [(right hand – left hand)/(right hand + left hand)] and multiplying the result by 100. A *consistency score* was also computed by averaging right hand performance of the four door lift tasks (scored 0, 1, 2, 3, or 4 out of 4; Bryden et al., 2007). Finally, a *bimanual score* was by recording whether the hand used to open the cabinet door was the same to retrieve the candy dispenser. A score of 1 was given if opposite hands were used, whereas a score of 2 was given if participants used the same hand for both elements of the task, for a total possible eight points.

RESULTS

HANDEDNESS IN TYPICAL DEVELOPMENT

The first stage of analysis examined the overall relationship between scores obtained by right-handers in the first and second session. This was done to assess how reliable the measures were across time. Correlation analysis revealed a significant positive relationship between laterality quotients computed from the WHQ, $r = 0.84$, $p < 0.01$, and AP, $r = 0.44$, $p < 0.01$. For the WHCT, significant positive relationships were revealed for the total ($r = 0.55$, $p < 0.01$), skilled ($r = 0.49$, $p < 0.01$), consistency ($r = 0.49$, $p < 0.01$), and bimanual ($r = 0.72$, $p < 0.01$) scores. For subsequent analysis, participants were split into six separate age groups (3- to 4-year-olds, 5- to 6-year-olds, 7- to 8-year-olds, 9- to 10-year-olds, 11- to 12-year-olds, and adults). The following will outline results derived from the WHQ, AP, and WatHand Cabinet tasks.

Waterloo Handedness Questionnaire

As 3- to 4-year-olds did not complete the WHQ, analysis was limited to 5- to 12-year-old children and adults. An analysis of variance (ANOVA) test was used to analyze laterality quotients computed form the WHQ as a factor of Age (x5: 5- to 6-, 7- to 8-, 9- to 10-, 11- to 12-year-olds, adults) and Session (x2: first session, second session). There was a main effect of Session [$F(1,78) = 9.933$, $p = 0.002$, $\eta^2 = 0.113$]. Laterality quotients were more positive in the second session ($M = 79.15$, $SD = 30.15$) in comparison to the first ($M = 73.00$, $SD = 31.49$). Neither a main effect of Age, nor a Session × Age interaction was revealed.

Annett pegboard

All participants completed the AP task. An ANOVA was used to assess laterality quotients computed (see **Figure 1**), as a function of Age (x6: 3- to 4-, 5- to 6-, 7- to 8-, 9- to 10-, 11- to 12-year-olds, adults), and Session (x2: first session, second session). There was a main effect of session [$F(1,88) = 3.971$, $p = 0.049$, $\eta^2 = 0.043$]. Laterality quotients were more positive (i.e., greater difference between the two hands favoring the right-hand] in the first session ($M = 5.91$, $SD = 4.79$) compared to the second ($M = 4.73$, $SE = 0.54$). There was also a main effect of age [$F(5,88) = 2.752$, $p = 0.023$, $\eta^2 = 0.135$]. *Post hoc* tests using a Bonferroni correction for multiple comparisons displayed the difference between 5- to 6-year-olds and 3- to 4-year-olds was not far from reaching statistical significance ($p = 0.090$), such that 5- to 6-year-olds displayed more positive laterality quotients (i.e., greater performance difference between the two hands favoring the right-hand) compared to 3- to 4-year-olds. A Session × Age interaction was not revealed.

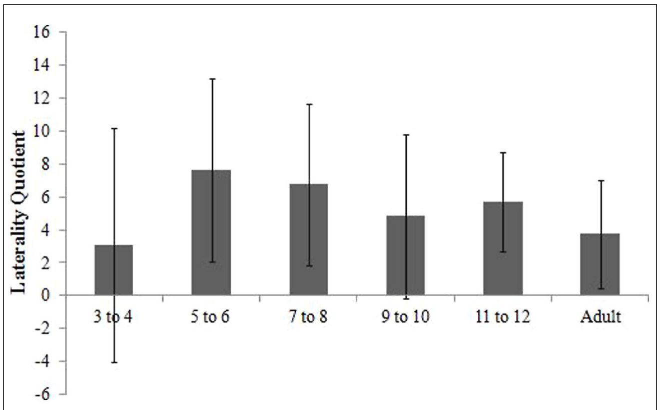

FIGURE 1 | Laterality quotients computed from typically-developing participants' Annett Pegboard Task.

WatHand Cabinet Test

Separate ANOVAs were performed for each of the four sub scores (total, skilled, consistency, and bimanual scores), as a function of Age (x6: 3- to 4-, 5- to 6-, 7- to 8-, 9- to 10-, 11- to 12-year-olds, adults), and Session (x2: first session, second session). No significant main effects or interactions were revealed for the total, skilled, and consistency score ($p < 0.05$). For the bimanual score (see **Figure 2**), there was a main effect of age [$F(5,88) = 8.956$, $p < 0.001$, $\eta^2 = 0.337$]. *Post hoc* tests using a Bonferroni correction for multiple comparisons displayed 3- to 4-year-olds had significantly higher scores than 7- to 12-year-olds and adults. There was no difference between 3- to 4- and 5- to 6-year-olds. The 5- to 6-year-olds had significantly higher scores than 11- to 12-year-olds and adults. This indicates that 3- to 4-year-olds were more likely than 7- to 12-year-olds and adults to lift the cabinet door and retrieve the object from within the cabinet with the same hand; whereas, 5- to 6-year-olds were more likely than 11- to 12-year-olds and adults to lift the cabinet door and retrieve the object from within the cabinet with the same hand.

CHILDREN WITH ASD AND THEIR TYPICALLY DEVELOPING PEERS

Thirteen children with ASD between the ages of 5 and 11 participated in this portion of the study. Two children did not complete the entire battery of tests on the second day of testing; therefore they were excluded from analysis. After data collection, two additional children were excluded from analysis because their AQ-Child scores were below the cut off of 76. The nine children with ASD (six male, three female, $M_{age} = 8.11$, $SD = 1.96$) remaining had a range of AQ total scores from 76 to 121 ($M_{score} = 98.67$, $SD = 13.11$). The WHQ identified one female participant as left handed ($score = -100$), whereas the remaining participants were right handed ($M_{score} = 97.60$, $SD = 4.70$).

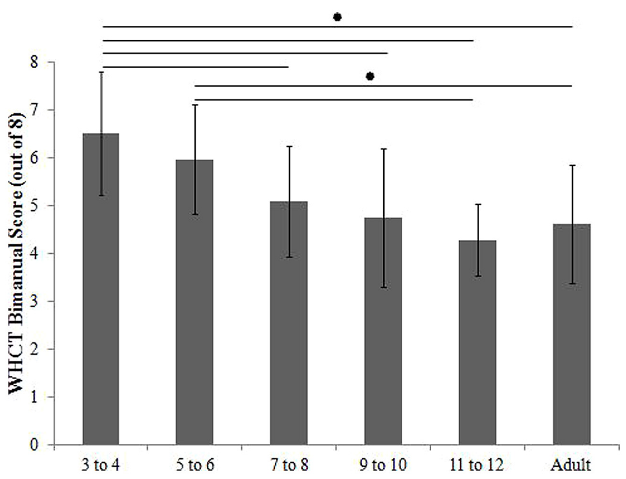

FIGURE 2 | Typically-developing participants' bimanual scores computed form the WatHand Cabinet Test.

Considering differences in the ratio of male to female and right to left participants in both groups (i.e., children with ASD and TD children), only right-handed male children were included, to match according to sex and comparable in chronological age. As such, analysis included six male children with ASD ($M_{age} = 7.50$, SD = 3.07; $M_{AQ-score} = 101.67$, SD = 10.13) and 24 TD children from the first sample ($M_{age} = 8.00$, SD = 1.98; **Table 2**). As mentioned previously, children with ASD were either unable or unwilling to complete the WHQ orally; therefore parents were asked to complete the questionnaire on behalf of their children on the first day of collection. As data was collected through different means, there was no way of comparing TD children and children with ASD directly; therefore WHQ data was only used to confirm self-report hand preference.

The first stage of analysis examined the overall relationship between scores obtained by children with ASD in the first and second session. This was done to assess how reliable the measures were across time in this sample of children. Correlation analysis revealed a non-significant negative correlation between laterality quotients computed from the AP, $r = -0.62$, $p = 0.19$. For the WHCT, significant positive relationships were revealed for the total ($r = 0.89$, $p < 0.05$) and consistency ($r = 0.89$, $p < 0.05$) scores. Skilled ($r = 0.77$, $p = 0.07$), and bimanual ($r = 0.55$, $p = 0.26$) scores were not correlated. Subsequent analyses compared the performance of children with ASD and their TD peers. The following section will outline the comparison between male right-handed TD children and children with ASD on the AP and WHCT. To help explain the high standard deviations, minimum and maximum scores are listed in **Table 3**.

Table 2 | Participant demographics – comparison between typically-developing (TD) children and children with ASD (ONLY RH male children included in analysis).

Group	*N*	Mean age (SD)
Children with ASD	6	7.50 (3.07)
TD Children	24	8.00 (1.98)

Table 3 | Minimum and maximum scores for TD children and children with ASD.

	TD Children		Children with ASD	
	Minimum	**Maximum**	**Minimum**	**Maximum**
Annett pegboard				
Session 1	−5.47	15.26	5.31	13.21
Session 2	−4.10	17.58	−5.79	6.85
WHCT total				
Session 1	−20.00	100.00	40.00	100.00
Session 2	−40.00	100.00	60.00	100.00
WHCT skilled				
Session 1	33.33	100.00	42.86	100.00
Session 2	14.29	100.00	71.43	100.00
WHCT consistency				
Session 1	0.00	4.00	3.00	2.00
Session 2	0.00	4.00	4.00	4.00
WHCT bimanual				
Session 1	4.00	8.00	4.00	8.00
Session 2	4.00	8.00	4.00	8.00

Annett pegboard

An ANOVA was used to assess laterality quotients computed from the AP (see **Figure 3**), as a function of Group (x2: TD children, children with ASD), and Session (x2: first session, second session). There was a main effect of Session [$F(1,28) = 8.686$, $p = 0.006$, $\eta^2 = 0.237$] and a Session × group interaction [$F(1,28) = 6.632$, $p = 0.016$, $\eta^2 = 0.191$]. Laterality quotients were more positive in the first session compared to the second; however, the Session × group interaction revealed this was due to children with ASD, who had more positive laterality quotients (i.e., greater difference between the two hands favoring the right-hand) in the first session. There was no main effect of group.

WatHand Cabinet Test

Separate ANOVAs were performed for each of the four sub scores (total, skilled, consistency, and bimanual scores), as a function of Group (x2: TD children, children with ASD), and Session (x2: first session, second session). No significant effects or interactions were revealed in analyses for the total, skilled, or consistency scores ($p > 0.05$). For the bimanual score, there was a main effect of Session [$F(1,28) = 6.760$, $p = 0.015$, $\eta^2 = 0.194$]. Bimanual scores were greater in the first session ($M = 5.229$, SD = 1.416) compared to the second ($M = 4.688$, SD = 1.095). No main effect of group or Session × group interaction emerged.

DISCUSSION

It is generally understood that young, TD children (3- to 4-year-olds) display weak hand preference tendencies. Furthermore, it is argued that hand preference is established at age 6 and strength

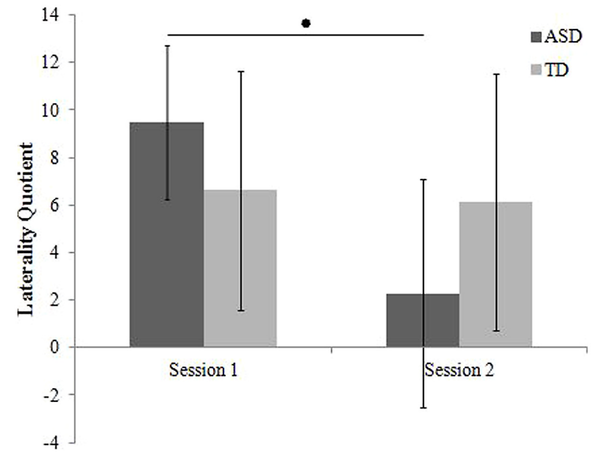

FIGURE 3 | Laterality quotients computed from the Annett Pegboard.

improves with age (see Scharoun and Bryden, 2014 for a review). At the age of 6 children are learning to write; therefore improved writing skills may explain an increase in the strength of hand preference with age (e.g., McManus et al., 1988). Observing children with ASD in comparison to their TD peers, variable hand selection strategies have been noted, such that children with ASD are described as having 'mixed-preference' or an overall pattern of non-right handedness (e.g., Cornish and McManus, 1996). Clearly *strength* of handedness is a topic that is continuously discussed in the handedness literature.

With that in mind, the current study addressed two specific research questions. First, does strength of handedness change over repeated testing sessions as a function of age? It was hypothesized that strength of handedness would be more reliably assessed over repeated testing sessions as a function of age. In other words, variability in performance would decrease as a function of age, such that younger children would display weak handedness tendencies, whereas older children would display stronger, and thus more reliably handedness tendencies. Secondly, is there a difference in strength of handedness when comparing TD children and children with ASD matched according to sex and comparable in chronological age? It was hypothesized that TD children would display stronger preference tendencies than children with ASD over repeated testing sessions. The following will discuss each research question and hypothesis in turn.

HANDEDNESS IN TYPICAL DEVELOPMENT

The Waterloo Handedness Questionnaire

Research to date outlines that right handed children report a reliable preference for the right hand, similar to adults (e.g., Bryden et al., 1991). In line with previous findings, an overall right hand preference was observed (Steenhuis and Bryden, 1989; Steenhuis et al., 1990). Interestingly, regardless of age, participants demonstrated a significantly stronger right hand preference during the second testing session. This was likely due to familiarity with the questions. Anecdotally, participants took longer to complete the questionnaire in the first session. It can be presumed that more thought was being put into answers.

The Annett pegboard

Previous research has displayed variable results with respect to performance on the AP. Some suggest that asymmetries do not change as a function of age (Kilshaw and Annett, 1983; Curt et al., 1992; Annett, 2002; Dellatolas et al., 2003). However, others (Roy et al., 2003; Bryden et al., 2007) have noted children display greater performance differences between the hands than adults. Results of the current study do not agree with either hypothesis. The difference between 5- to 6-year-olds and 3- to 4-year-olds was not far from reaching statistical significance ($p = 0.090$). The 5- to 6-year-olds displayed more positive laterality quotients (i.e., greater performance difference between the two hands favoring the right-hand) compared to 3- to 4-year-olds. No other differences between age groups were noted. These results provide partial support for Annett (2002), who described that, "differences are slightly larger in young than older children but this is a function of the rapid rates of growth in the early years" (p. 552). This does not explain the performance of 3- to 4-year-olds.

Bryden et al. (2000a) have suggested that young TD children (3- to 4-year-olds) are the least lateralized and therefore display minimal performance differences between the hands. By age 6, however, "handedness has been firmly entrenched" (Bryden et al., 2000b, p. 64). Pryde et al. (2000) have proposed that older children (i.e., 6- to 10-year-olds) "tend to think in concrete, inflexible terms and are undergoing a period of motor skill refinement" (p. 374). As such, older children are described as showing an overuse of the preferred hand. In other words, reliably use their preferred hand, regardless of task, or region of space. In line with this idea, it is likely that, due to weak hand preference 3- to 4-year-olds displayed small performance differences between the two hands (Annett, 2002; Dellatolas et al., 2003). As hand preference is typically established at age 6 (Bryden et al., 2000b), this likely explains why 5- to 6-year-olds displayed large performance differences between the two hands, in favor of the preferred hand. De Agostini et al. (1992) observed a greater proportion of mixed-handed children at age 3 than at age 6. They explained that "the decreasing percentage of mixed-handed children with age contributed to the increase of full right-handed children" (p. 53). According to Fennell et al. (1983), hand preference at age 5 predicted handedness for 97% of right-handers at age 11. It is thus likely that a right-hand was established in the 5- to 6-year-olds in this study, whereas 3- to 4-year-olds displayed more of a mixed-preference.

The WatHand Cabinet Test

Performance measures, like the AP, have inherent limitations, as they only measure one aspect of handedness – in this case, speed. The WHCT, an observational-based assessment, has been shown to be the most accurate predictor of hand preference (Brown et al., 2004), especially for use with children (Bryden et al., 2007). That said, previous studies have based their conclusions on a single testing session (e.g., Brown et al., 2004; Bryden et al., 2007); whereas the current study was completed on two repeated testing days, in order to measure if handedness can be reliably assessed with this task. Paralleling previous studies (e.g., Bryden et al., 2007), four sub-scores were computed: a total score, skilled score, consistency score, and bimanual score. No significant main effects or interactions were revealed for the total, skilled or consistency score with respect to age or session. This indicates right handed children reliably display a preference for one hand within these tasks. For the bimanual score, 3- to 4-year-olds had the highest scores. Thus, they were more likely to lift the cabinet door and retrieve the object from within the cabinet with the same hand, whereas older children and adults used. This result is in line with a previous report from Bryden et al. (2007) who noted younger children showed a stronger preference for the preferred hand. However, in Bryden et al.'s (2007) study, this was true for 3- to 9-year-old children, where this was limited to 3- to 4-year-olds in the current study. Bryden et al. (2007) suggest that "it may be that the two tasks (opening a door and picking up an object) were not considered motorically complex enough to drive the selection of the preferred hand for older individuals" (p. 840) and that "experience could have decreased the older participants reliance on the preferred hand" (p. 840–841). That said, it may also be a function of corpus callosum maturation. With age, there is an evident transition from a unimanual strategy to a bimanual strategy (e.g., Fagard and Corroyer, 2003).

HANDEDNESS IN ASD

The second objective of this study was to investigate whether a group of children with ASD demonstrate the same strength of handedness as their TD peers, as variable hand preference tendencies have been reported within performance of a single task (e.g., McManus et al., 1992; Cornish and McManus, 1996; Markoulakis et al., 2012). Based on previous reports in the literature, it was hypothesized that children with ASD would demonstrate variable hand use strategies in comparison to their TD counterparts. In partial agreement with previous findings, the current study did observe some evidence of variable hand use tendencies in children with ASD (e.g., McManus et al., 1992; Cornish and McManus, 1996; Markoulakis et al., 2012), although this was limited.

The Annett pegboard

In the current study, there was no statistically significant difference between children with ASD and their TD counterparts. These results are in line with previous reports in the literature which indicate that performance differences between TD children and children with ASD typically subside when measuring the difference between the two hands using laterality quotients (Cornish and McManus, 1996). This study adds to the literature, suggesting that this extends to assessment over repeated sessions. That said, correlation analysis revealed a non-significant negative correlation between AP scores in the first and second session. This suggests that, as a group, children with ASD do display more variable handedness.

The WatHand Cabinet Test

Results of this study revealed no differences between children with ASD and their TD peers in any of the sub-scores of the WHCT (i.e., total score, skilled score, consistency score, and bimanual score). These findings opposed those found recently in the literature by Markoulakis et al. (2012), who noted variable hand-use strategies in one testing session.

SUMMARY AND CONCLUSION

The first research question asked if strength of handedness changes over repeated testing sessions as a function of age. With respect to hand preference, results from the WHQ contrasted the hypothesis, but were in line with previous reports which note that, similar to adults, children report a reliable preference for the right hand (Bryden et al., 1991). That said, significantly stronger right hand preference was seen in the second session, which begs the question of how familiarity with the questions influences participant response. Next, the WHCT, a performance-based assessment of preference, revealed that 3- to 4-year-olds had higher bimanual scores than all other age groups. This was again in contrast with the hypothesis, but in line with Bryden et al. (2007) who noted that the task may not be complex enough to drive preferred hand selection in older participants. Adding to the literature, there were no differences in hand use preferences between sessions; providing evidence that the WHCT is a reliable measure. Finally, with respect to the AP, the measure of performance used in the study, a marginally significant difference was revealed between 3- to 4- and 5- to 6-year-olds, where 5- to 6-year-olds displayed greater performance differences between the two hands favoring the right-hand. As 3- to 4-year-olds are known to display weak hand preference tendencies, and hand preference is known to be entrenched by the age of 6 (Bryden et al., 2000a), this result is also in line with previous reports. Summarizing then, results of this study provide additional evidence to support the notion that 3- to 4-year-olds show weaker handedness in comparison to older children and adults. Thus it is clear that, despite weak tendencies within a session, children in this age group reliably display a weak pattern of handedness from one session to the next.

The second research question asked if a difference in strength of handedness is evident when comparing TD children and children with ASD matched according to sex and comparable in chronological age. Results were in partial support of the the hypothesis, such that there was no difference between TD children and children with ASD within each of the tasks, or between repeated testing sessions; however, performance of the AP revealed children with ASD displayed more variable handedness, exemplified by more positive laterality quotients in the first session, compared to the second. This was in contrast to TD children who demonstrated reliable strength in handedness.

Results of this study must be interpreted in light of limitations. In particular, this study included a small group of children with ASD, in comparison to a large group of TD controls. Comparison was limited to self-report right-handed male children matched according to sex and comparable in chronological age. It is thus possible that differences may be attributed to children's IQ even though children were identified as high-functioning prior to their participation in this study. In conclusion, results of this study identify the need for continued examination of hand preference and motor skills in children with ASD. It has been argued that motor deficits are a cardinal feature of ASD (Fournier et al., 2010), are more common than in TD individuals (Matson and Kozlowski, 2011) and may significantly affect social development and overall quality of life (Gowen and Hamilton, 2013). However, variable performance is commonly reported and the etiology remains unclear (Gowen and Hamilton, 2013). Clearly, future research is warranted.

ACKNOWLEDGMENTS

The authors would like to acknowledge the Natural Sciences and Engineering Research Council of Canada for funding this project (Pamela J. Bryden) and the Autism Research Centre (ARC) for access to the Autism Spectrum Question: Children's Version and scoring key. This project was completed as part of a master's thesis (Sara M. Scharoun). This paper was presented at the North American Society for the Psychology of Sport and Physical Activity (NASPSPA) conference in New Orleans, LA, USA (June 13–15, 2013).

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 16 September 2014; accepted: 06 January 2015; published online: 03 February 2015.

Citation: Scharoun SM and Bryden PJ (2015) Is strength of handedness reliable over repeated testing? An examination of typical development and autism spectrum disorder. Front. Psychol. ***6****:17. doi: 10.3389/fpsyg.2015.00017*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

MINI REVIEW ARTICLE
published: 15 December 2014
doi: 10.3389/fpsyg.2014.01480

Manual (a)symmetries in grasp posture planning: a short review

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Many activities of daily living require that we physically interact with one or more objects. Object manipulation provides an intriguing domain in which the presence and extent of manual asymmetries can be studied on a motor planning and a motor execution level. In this literature review we present a state of the art for manual asymmetries at the level of motor planning during object manipulation. First, we introduce pioneering work on grasp posture planning. We then sketch the studies investigating the impact of future task demands during unimanual and bimanual object manipulation tasks in healthy adult populations. In sum, in contrast to motor execution, there is little evidence for hand-based performance differences in grasp posture planning. We discuss potential reasons for the lack of manual asymmetries in motor planning and outline potential avenues of future research.

Keywords: manual asymmetries, grasping, motor planning, end-state comfort, bimanual coordination

INTRODUCTION

The study of differences in the performance capabilities of the two hands, commonly referred to as manual asymmetries, has long been a topic of intense study among researchers from fields such as psychology, neurophysiology, and motor control (see Goble and Brown, 2008, for a review). It is commonly accepted that humans prefer to use one hand over the other when performing manual everyday tasks (e.g., writing or grasping an object), with the majority of people (about 90% of the population) exhibiting a preference to use the right hand over the left (Coren and Porac, 1977). Considering the performance of the two hands, it has been reported that task performance with the dominant hand is often superior compared to the non-dominant hand. For example, the dominant arm of right-handed individuals can produce greater forces than the non-dominant hand (e.g., Petersen et al., 1989; Armstrong and Oldham, 1999), is faster and more consistent during repetitive finger tapping (Peters, 1976; Todor and Kyprie, 1980; Todor et al., 1982) and is more accurate during reaching and rapid aiming movements (Annett et al., 1979; Roy and Elliott, 1989; Carson et al., 1993).

Investigations into manual asymmetries are not limited to the level of motor execution but have also been extended to the motor planning level. One intriguing domain in which motor planning can be studied is object manipulation (see Rosenbaum et al., 2012, 2013, for reviews). As the very same object can be grasped differently depending on whether one intends to use that object or to pass it to another person to use, differences in the way an object is grasped depending on different future task demands or action goals can be ascribed to differences in the respective action plans. In addition, object manipulation provides the opportunity to study motor planning of different orders (Rosenbaum et al., 2012). Whereas first-order planning reflects adjustments of grasp postures to immediate task demands (e.g., object orientation, shape, and size), second-order planning reflects adjustments that not only consider immediately available perceptual information but also incorporate demands of the next task to be performed.

In this article, we review current research on second-order motor planning during object manipulation tasks (i.e., grasping an object with *one* subsequent displacement), with a focus on the impact that future task demands elicit on the presence of manual asymmetries.

PIONEERING WORK

The foundation of second-order motor planning in the context of object manipulation was inspired by a natural observation David A. Rosenbaum made in a restaurant where he observed a waiter pouring water into drinking glasses. The glasses stood inverted on the table. To fill each glass with water, the waiter initially grasped it with a (presumably uncomfortable) thumb-down grip, turned it by 180° to set it down with a (comfortable) thumb-up grip. Rosenbaum et al. (1990) transferred this observation to the laboratory. The setup used in this study – which has become known as the 'bar-transport task' – consisted of a wooden bar which was horizontally arranged on a cradle such that participants could grasp it using either an overhand grasp or an underhand grasp. Participants grasped the bar and rotated it 90° to place either its left or right end into a target disk located to the left or right side. The authors found that, regardless of target location, the selection of initial grasp posture (i.e., underhand or overhand grasp) depended on the required end orientation of the bar. Specifically, participants adopted an initial overhand grasp posture when using the dominant right hand to place the right end of the bar into the target disk. Conversely, when the left end of the bar was to be placed into the target disk, participants initially grasped the bar with an underhand grasp. Thus, participants always selected an initial grasp that afforded a comfortable thumb-up posture at the end of the movement. Termed the end-state comfort effect, this phenomenon indicates that participants represent future posture states and plan their initial grasps in anticipation of these future postures prior to movement execution. The end-state comfort effect provides a nice tool to study motor planning processes and it has been applied in a variety of different tasks (e.g., Cohen and Rosenbaum, 2004; Herbort and Butz, 2010, 2012; Hughes et al., 2012c). Consequently, the end-state comfort effect is also an instrument to examine whether manual asymmetries are evident on a motor planning level during unimanual and bimanual object manipulation tasks. Work on these topics will form the focus of the following two sections.

UNIMANUAL TASKS

In the Rosenbaum et al. (1990) study participants were initially not told which hand to use when performing the task. The authors reported that out of the 12 participants, six participants used only their right hand, one participant used only the left hand, and the remaining five participants switched hands between trials. Nevertheless, independent of hand choice, participants always selected initial grasp posture that were in accordance with the end-state comfort effect. Thus, left hand performance mirrored right-hand performance. Similar results using the bar-transport task were obtained by Weigelt et al. (2006; see **Figure 1**).

In a later study, Rosenbaum et al. (1993) employed a task that allowed for a more fine-grained measure of motor planning performance. The experimental setup consisted of a handle connected to a disk. A small cardboard tab was attached to the disk such that rotating the handle caused the disk and the tab to turn. The tab covered one of eight target position which were arranged around the disk (separated by 45°). In this task, participants grasped and turned the handle such that the tab would cover a designated target, and each possible combination of start and end position were tested. Confirming the results of the original bar-transport task, initial grasp postures depended on the final target position and were selected to afford a comfortable end posture. Again, there was no evidence for manual asymmetries in motor planning as left-hand performance mirrored that of the right hand.

Subsequent research on grasp posture planning during unimanual object manipulation tasks has also reported equal performance between hands (Hughes and Franz, 2008; Herbort and Butz, 2011; Hughes et al., 2011b, 2012a; Seegelke et al., 2011; see **Figure 1**). For example, in the first study specifically conducted to investigate the presence and extent of manual asymmetries on motor planning (Seegelke et al., 2011), participants grasped a vertically oriented cylinder with the dominant right hand, or the non-dominant left hand, and placed it to a target located to the left or right side of the object's start position. Thus, in contrast to the original bar-transport task which necessitated always 90° object rotation, in this paradigm the object was to be placed vertically to the targets such that it required either no rotation or 180° rotation, depending on condition. Based on the literature regarding manual asymmetries in motor execution (cf. Elliott and Chua, 1996), it was hypothesized that the dominant right hand should exhibit a greater preference for comfortable end postures than the non-dominant left hand. In that study it was observed that initial

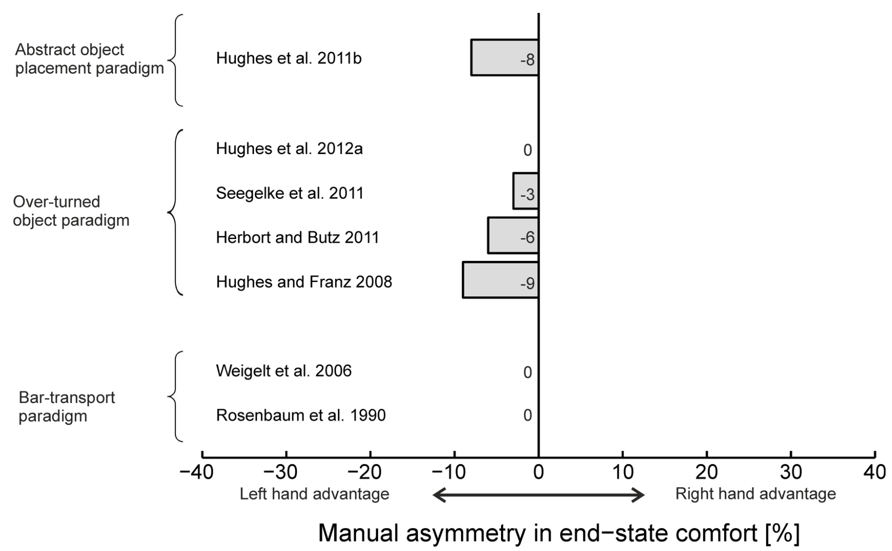

FIGURE 1 | Assessment of manual asymmetries in end-state comfort in unimanual tasks. Negative values indicate higher end-state comfort for the left hand, positive values indicate higher end-state comfort for the right hand. For Herbort and Butz (2011) values are based on participants who exclusively used thumb-up and thumb-down grasps. Results from Rosenbaum et al. (1993) are not shown as no exact values are presented in this paper.

grasp selection was strongly influenced by target location and the required object end-orientation. However, the hypothesis regarding manual asymmetries was not confirmed. Regardless of target location or the hand used to move the object participants almost always used a thumb-up grasp posture during trials in which the object required no rotation. During trials that required 180° object rotation trials, it was found that end-state comfort satisfaction was significantly more pronounced for the contralateral target location for both the dominant and the non-dominant hand. Analogous to the well-established notion that spatial precision demands affect the presence and extent of manual asymmetries during motor execution (e.g., Bryden and Roy, 1999; Bryden et al., 2007; van Doorn, 2008), it was reasoned that the absence of manual asymmetries might be rooted in the relatively low precision requirements of the task.

However, this explanation was soon rendered unlikely by a subsequent study in which the precision demands at the start and the end of the movement were manipulated (Hughes et al., 2012a). In this task, participants grasped a vertically arranged cylinder located in a start disk with the left or right hand and placed it vertically to a target disk with either no or 180° object rotation. The diameter of the start and target disks were manipulated so that the precision requirements were either identical (low initial and final precision, high initial and final precision) or different (low initial high final precision, high initial low final precision). The general finding was that half of the participants (precision-sensitive group) adjusted their initial grasps depending on the precision requirements of the task (i.e., they adopted comfortable postures at the position where the precision demands were high), whereas the other half (end-state comfort consistent group) planned their movements such that they would satisfy end-state comfort regardless of precision demands. However, and of greater importance for the purpose of this review, there were no differences in grasp choice between the dominant right and the non-dominant left hand for either subset of participants (overall end-state comfort satisfaction: precision-sensitive: left hand 64%, right hand 62%; end-state comfort consistent group: left hand 97%, right hand 99%). Taken together, the results from this study provide evidence that precision demands do not affect manual asymmetries on a motor planning level.

In another study (Herbort and Butz, 2011), participants grasped an upright or inverted cup with either the dominant right or the non-dominant left hand and rotated it by 180° before placing it on the target circle. The authors found that initial cup orientation significantly affected grasp choice. Inverted cups were grasped more frequently with an initial thumb-down grasp whereas upright cups were grasped more often with an initial thumb-up grasp. However, the hand used for object manipulation did not affect grasp choice for either the upright or inverted cup orientation. It was argued that the inability to detect manual asymmetries might be due to the low complexity level of their task, or that participants had to interact with a common everyday object (i.e., a drinking cup), for which stereotypic (habitual) solutions already exist. The authors postulated that more complex actions – for example bimanual actions – might provide a more suitable situation in which potential hand-based differences in motor planning may be observed.

BIMANUAL TASKS

A number of researchers have been interested in whether the end-state comfort effect would extend to movements made with the two hands (Fischman et al., 2003; Weigelt et al., 2006; Hughes and Franz, 2008; van der Wel and Rosenbaum, 2010; Hughes et al., 2011a,b). Bimanual movements provide an interesting scenario in which to examine grasp posture planning, as the sensitivity toward end-state comfort often competes with the strong tendency for the two hands to grasp objects with identical postures (bimanual spatial coupling).

The first report of manual asymmetries in bimanual movements on a motor planning level came from the work of Janssen et al. (2009). In this study, participants simultaneously grasped two CD casings (one with each hand) from two lower boxes and place them into two upper boxes. The authors manipulated the start and end orientation of each CD (horizontal or vertical), the start and end orientation congruency (congruent: both CDs horizontal or vertical; incongruent: one CD horizontal, one CD vertical) and the required object rotation (0°, 90° supination, 90° pronation, 180°). The experiment was designed such that one CD always required 180° rotation while the other required 0°, 90° supination or 90° pronation. Janssen et al. (2009) found that the tendency of right-handed individuals to avoid uncomfortable end-postures was higher and more variable for the right hand (82.0%, SD = 20.2%) than for the left hand (49.8%, SD = 9.8%). However, the sensitivity toward end-state comfort was strongly influenced by object end-orientation, such that the tendency to avoid uncomfortable end-postures was higher when the CD was to be placed in a vertical (80.8%, SD = 11.3%), than in a horizontal end-orientation (61.9%, SD = 15.7%). Janssen et al. (2009) argued that the presence of manual asymmetries observed in their study arose from the increased complexity of the CD placement task compared to the bar transport paradigms used in previous studies that either did not observe or failed to report the presence of manual asymmetries (Fischman et al., 2003; Weigelt et al., 2006). This increased complexity resulted in a breakdown of overall anticipatory planning performance with participants prioritizing end-state comfort planning for the dominant right hand.

The authors posited that the observed manual asymmetries in end-state comfort compliance occurred because of differences in hemispheric specializations with respect to motor planning, and tested this *left-hemisphere dominance for motor planning hypothesis* by asking left-hand dominant individuals to perform the CD placing task (Janssen et al., 2011). As in their previous study (Janssen et al., 2009) they found that end-state comfort was more pronounced for the right hand, compared to the left hand, especially during movements to horizontal end-orientations. The similarity between both handedness groups was congruent with the expectations of the left-hemisphere dominance for motor planning hypothesis, hereby bolstering the claim that motor planning is a specialized function of the left hemisphere (Kim et al., 1993; Haaland et al., 2000; Frey, 2008).

Motivated in part by the results of Janssen et al. (2009, 2011), Hughes et al. (2011a) explored hemispheric differences in motor planning and execution in left- and right-handed individuals in a grasping and placing task in which participants grasped two objects from a table and placed them on a board to one of four end-orientations (0°, 90° internal rotation, 180° rotation, 90° external rotation). Manual asymmetries in motor execution were observed, with shorter object transport times observed for the left hand, regardless of handedness. However, contrary to the left hemisphere dominance motion planning hypothesis, end-state comfort sensitivity was similar for both the non-dominant and dominant hand, regardless of whether the individuals were left- or right-handed.

Hughes et al. (2011a) suggested that the discrepancy in results between Janssen et al. (2009, 2011) and their study arose due to differences in task paradigm. In the grasping and placing paradigm we employed, participants were required to place the objects on a fitting board, whereas in the studies of Janssen et al. (2009, 2011) participants placed a CD casing into a box. Thus, it could be argued that the CD placing task required a higher level of precision at the end of the movement than placing an object on a fitting board, and that the planning of initial grasp postures is influenced by the precision demands of the task. The authors argued that this hypothesis was unlikely to account for differences across paradigms, as participants in Hughes et al. (2011a) were very accurate when placing the object on the fitting board, and other studies that also employed high precision tasks (e.g., Weigelt et al., 2006) reported that participants almost always complied with end-state comfort, regardless of hand. Based on these pieces of evidence Hughes et al. (2011a) mentioned the possibility that the manual asymmetries in motor planning were specific to the CD placement task and paradigm.

While this latter issue is still open for debate, considering all literature on bimanual end-state comfort available at the present time, there is little evidence to support the existence of manual asymmetries at the motor planning level. Besides the higher end-state comfort values for the right hand in the CD placement task (Janssen et al., 2009, 2011), similar end-state comfort compliance for the two hands have been reported in the following bimanual paradigms: bar transport paradigm (Fischman et al., 2003; Weigelt et al., 2006; Hughes and Seegelke, 2013), plunger transport paradigm (van der Wel and Rosenbaum, 2010), over-turned object paradigm (Hughes and Franz, 2008), bar-and-spoon rotation paradigm (Janssen et al., 2010), and abstract object placement paradigm (Hughes et al., 2011a,b, 2012b, 2014; see **Figure 2**).

CONCLUSION

In this short review we found little evidence for hand-based performance differences in grasp posture planning during second-order object manipulation tasks in healthy adults. These observations are in contrast to the routinely reported presence of manual asymmetries on the level of motor execution. Motor planning and motor execution constitute different (though temporally overlapping) stages of human motor behavior (see Glover, 2004, for a review), and there exists considerable evidence from behavioral (e.g., Woodworth, 1899; Keele and Posner, 1968; Meyer et al., 1988) and neurophysiological studies demonstrating a functional distinction between these two stages (e.g., Grol et al., 2007; Glover et al., 2012; Begliomini et al., 2014). Given this differentiation, it seems reasonable to assume that task constraints known to influence manual asymmetries during motor execution [e.g., precision demands of the task (Bryden and Roy, 1999; Bryden et al., 2007), task complexity (cf. Bryden, 2000)] may not equally affect performance differences between the hands on the level of motor planning.

It has been argued that motor planning of complex actions (i.e., actions beyond simple reaching and pointing) involves decisions

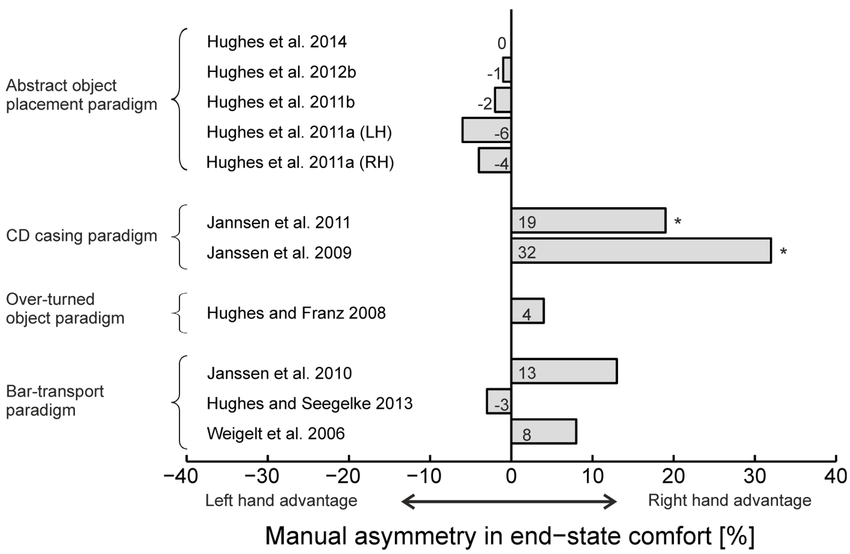

FIGURE 2 | Assessment of manual asymmetries in end-state comfort in bimanual tasks. Negative values indicate higher end-state comfort for the left hand, positive values indicate higher end-state comfort for the right hand. Asterisks indicate significant differences between the hands. LH = left handers, RH = right handers. Results from Fischman et al. (2003) and van der Wel and Rosenbaum (2010) are not shown as no exact values are presented in these papers.

about the shape of the trajectory in an effector-independent manner (i.e., abstract kinematics; see Wong et al., 2014). The existence of such abstract goal representations has received support from numerous behavioral and neurophysiological studies (e.g., Keele, 1981; Wright, 1990; Castiello and Stelmach, 1993; Rijntjes et al., 1999; Wing, 2000; van der Wel et al., 2007; Albert and Ivry, 2009; Fu et al., 2010; Swinnen et al., 2010; Sartori et al., 2013) and is encompassed by the notion of *motor equivalence* – the capability of the motor system to achieve the same action goal by different means (Lashley, 1930, 1933; see also Bernstein, 1941). Consequently, the equal performance capabilities of the two hands suggest that decisions about which grasp posture to adopt are done without considering the effector used to execute that action, and reflect hand-independent motor planning processes at high levels of the motor hierarchy that are engraved through lifelong practice.

Alternatively, it is possible that the insensitivity of the measures may have masked manual asymmetries in grasp planning. The bulk of the studies conducted so far examined grasp posture planning using a binary grasp choice (i.e., participants could adopt only one of two grasps; e.g., underhand vs. overhand; thumb-down vs. thumb-up). As such, it is possible that manual asymmetries in grasp posture planning may be detected (if indeed they do exist) by employing continuous instead of binary measures of grasp selection (e.g., Cohen and Rosenbaum, 2004; Herbort and Butz, 2010, 2012; Seegelke et al., 2012, 2013a,b). Furthermore, research on populations with lateralized brain damage can provide intriguing insights into hemispheric specialization in motor planning in the context of object manipulation (e.g., Hermsdörfer et al., 1999; Steenbergen et al., 2000, 2004; Crajé et al., 2009). Interestingly, recent developments in cognitive robotics have opened up new opportunities to examine principles of motor planning in bimanual action. From our point of view, research in motor control can benefit from the advances in technological systems to enhance the understanding of human motor control in skilled unimanual and bimanual voluntary action (e.g., Schack and Ritter, 2013).

ACKNOWLEDGMENTS

This research was funded by the German Research Foundation (DFG EXC 277). We acknowledge support for the Article Processing Charge by the Deutsche Forschungsgemeinschaft and the Open Access Publication Funds of Bielefeld University Library.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 26 September 2014; accepted: 01 December 2014; published online: 15 December 2014.
*Citation: Seegelke C, Hughes CML and Schack T (2014) Manual (a)symmetries in grasp posture planning: a short review. Front. Psychol. **5**:1480. doi: 10.3389/fpsyg.2014.01480*
This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 10 February 2015
doi: 10.3389/fpsyg.2015.00092

The effect of endpoint congruency on bimanual transport and rotation tasks

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The completion of many goal oriented skills requires the tight coordination of the right and left hands to achieve the task objective. Although the coordination of wrist transport and orientation of the hand before object contact has been studied in detail for discrete bimanual tasks, as yet, very few studies have examined bimanual coordination when the target is already in hand. It has been shown that congruency of the goal facilitates the production of discrete bimanual responses. The purpose of this study was to investigate the role of goal congruency on precision bimanual transport and rotate tasks. In the current investigation, participants transported two cubic objects while rotating them laterally to place them into tight-fitting targets. The magnitude of the rotation could be the same for both hands (i.e., both 45 or 90°) or different (i.e., one 45 and 90°) and the endpoint orientations (i.e., goal) could either be congruent or incongruent. Results indicated that when the endpoint orientation was congruent for the two hands, movement times were similar regardless of hand (left or right), rotation magnitude (45, 90°) and whether the rotation magnitude for the two hands was the same or different. These results suggest that congruency of the endpoint goal facilitates the temporal synchronization of the transport component for two limbs. In contrast, a different pattern of results was obtained when considering the rotation component. Specifically, regardless of whether the hands were rotating the same magnitude or ending in congruent endpoint positions, the coordination of the rotation component between the hands was asynchronous. We hypothesize that the greater requirement to shift visual fixation from one hand/target to the other to ascertain the separate goal orientations may explain these differences. These results provide further evidence that multiple constraints act to influence the performance of skilled bimanual tasks.

Keywords: bimanual movements, movement synchrony, motor planning, movement constraints, endpoint congruency

INTRODUCTION

The performance of many goal oriented skills requires the tight coordination of the right and left hands to achieve the task objective. Consider tying your shoelaces or opening the cupboard door with your right hand while grasping a cup with your left hand. These tasks require precise spatial and temporal coordination between the two hands for the goal of the task to be successfully achieved.

Bimanual performance has received much attention in recent years, with several studies investigating how movements are planned based on direct or indirect spatial cues (Diedrichsen et al., 2003), how they are temporally and spatially coupled (Kelso et al., 1979; Franz et al., 1991, 2001; Dohle et al., 2000) and how movements are altered based on visual feedback (Bingham et al., 2008; Mason, 2008; Srinivasan and Martin, 2012). Recently Srinivasan and Martin (2012) have shown that with practice on a bimanual reaching task, participants begin to prioritize one hand over the other. Their results indicated that for their group of participants, the left hand became the primary hand, with gaze biased in that direction. Further, left-hand kinematics remained similar in unimanual and bimanual trials, while right-hand kinematics varied with task constraints. Although these studies have provided important descriptions of bimanual performance, they have focused almost exclusively on the planning and performance of movements prior to object contact. For most functional tasks, object manipulation does not end when the object is acquired, therefore a thorough investigation of coordination during the object manipulation phase of the movement is required.

In a previous series of studies, we investigated the coordination and concurrency of bimanual movements made by participants to simultaneously transport, rotate and place two objects into target wells (Mason and Bryden, 2007). The target wells were oriented such that participants had to rotate the objects 45 or 90° to achieve the task goal. Results indicated that the two hands were tightly synchronized when the two movements being performed required the same rotation. Specifically, transport and rotation movements for the two hands started and ended at the same time. However, when participants performed bimanual movements where the rotations were different, synchronization between the two hands was weaker and was influenced by the type of rotation being performed by each hand. The hand rotating to a 45° target ended the transport component later and the rotation component earlier than the hand moving to the 90° target. Further, the hand performing the 45° rotation committed a larger number of over-rotations than the hand performing the 90° rotation, resulting in less efficiency in the movement when compared to the unimanual conditions. These results suggest that movement symmetry acts as a constraint to significantly influence the planning and performance of bimanual skills.

Another constraint that has recently been shown to significantly influence and facilitate the production of discrete bimanual responses is the congruency of the endpoint goal (Kunde and Weigelt, 2005; Kunde et al., 2009; Hughes et al., 2011). Using a task inspired by Rosenbaum et al. (1990), Kunde and Weigelt (2005) investigated whether goal symmetry or movement symmetry has a greater influence on bimanual task performance. They manipulated goal congruency by asking participants to place objects in either parallel (i.e., both upright or both upside down) or opposite (i.e., one upright, one upside down) orientations. These goals could be achieved by either mirror-symmetrical (i.e., both hands turning inward or outward) or mirror-asymmetrical (i.e., one hand turns inward, one hand turns outward) movements. The authors suggested that if movement symmetry dominates the planning and performance of bimanual movements, performance would be better for mirror-symmetric movements regardless of endpoint goal congruency. In contrast, if endpoint goal was more important, then better performance would be exhibited with congruent endpoint goals regardless of movement symmetry. Their results indicated that reaction times, approach times, and manipulation times were strongly influenced by goal congruency but were not significantly influenced by movement symmetry. This led the authors to conclude that goal congruency (i.e., the "what" of actions) is crucial to motor planning and performance whereas the motor patterns used to achieve these goals (i.e., the "how" of actions) is less important. While the dominance of goal congruency over movement symmetry has been replicated (e.g., Weigelt et al., 2006), other studies have found mixed results. Specifically, Janssen et al. (2009) found the result, but only for the right hand. Others have reported that there is no preference for end-state planning over movement symmetry (Fischman et al., 2003; Hughes and Franz, 2008; Huhn et al., 2014). These conflicting results have led researchers to suggest that multiple planning constraints interact to allow flexibility in motor behavior in a dynamic and task dependent manner (van der Wel and Rosenbaum, 2010; Huhn et al., 2014).

In our previous studies (Mason and Bryden, 2007) the grasped targets always had spatially congruent start positions. This meant that asymmetric bimanual rotations also resulted in incongruent goal positions. Therefore, rotation magnitude (i.e., movement symmetry) and endpoint congruency were confounded. As such, we were not able to determine whether goal congruency plays a role in movement planning and execution for our task. Our task differs from those used by others studying constraints in movement planning in two respects. First, our task required both the transport of a grasped object toward a target location as well as the rotation of the object to place it in a target well. It is possible that each component of the movement (transport vs. rotation) might be influenced differentially by task constraints. This notion follows from work in reach-to-grasp movements where it has been shown that certain environmental constraints influence the transport but not the grasp or vice versa in a task dependent way (Gentilucci et al., 1991; Carnahan and McFadyen, 1996). The second difference in our paradigm when compared to previous work is the increased precision requirement inherent in the final goal. Specifically, in previous works, participants either rotated dowels to place them with a specific end facing upward or grasped plungers to move them to higher or lower shelves (Fischman et al., 2003; Kunde and Weigelt, 2005; Hughes and Franz, 2008; Huhn et al., 2014). In these paradigms, the precision required to successfully place the object at the end location was relatively low. In contrast, in our paradigm, participants need to precisely rotate the object in order to fit it into a tight target well. Thus, the increased precision requirements in both the movement and the end-goal introduce an additional constraint on the task that could supersede other constraints.

The purpose of this study was to investigate how movement and goal congruency interact to influence the transport and grasp components of a grasp and place task when precision requirements are high. By manipulating the congruency of the starting orientations, the endpoints (i.e., goal) could be congruent or incongruent for a given set of rotations. With these manipulations, we could determine whether decreases in movement synchrony are still observed in asymmetric conditions regardless of goal congruency. This result would suggest that precision requirements reduce the beneficial effects of goal congruency. In contrast, if movement synchrony was observed in asymmetric rotation conditions for the congruent endpoints, this would suggest that goal congruency is an important planning variable regardless of precision requirements.

MATERIALS AND METHODS

PARTICIPANTS

Twelve participants (six female, six male) with a mean age of 21.4 (range: 20–27) years participated in this study. All participants were right-hand dominant as assessed by the Waterloo Handedness Questionnaire (Bryden, 1977). Ethical approval from the University of Wisconsin–Madison Social and Behavioral Sciences Institutional Review Board and the Research Ethics Board at Wilfrid Laurier University was obtained before testing began. Participants had no prior knowledge of the experiment and were asked to provide informed consent before beginning the study. Each participant performed in one experimental session for approximately one half hour.

APPARATUS

Participants were seated facing a table on which a 48 cm × 96 cm sheet of medium density fiberboard (MDF) was fastened. A 15 cm × 59 cm rectangle was cut out of the sheet of MDF such that interchangeable target plates could be positioned in the rectangular cutout (see **Figure 1A**).

Kinematic data were recorded for the participants' hand movements using a VisualEyez 3000 (Phoenix Technologies Inc.) three-dimensional motion capture system. The VisualEyez camera monitored the position of light emitting diodes (LEDs) placed on

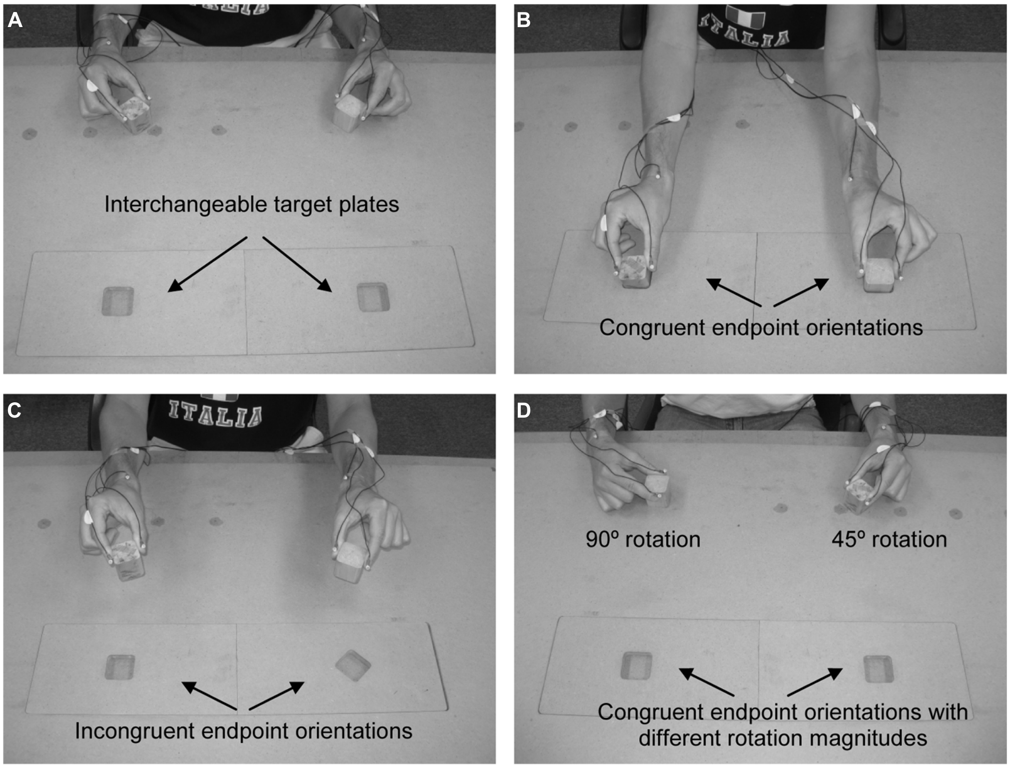


FIGURE 1 | General layout of experimental setup. Target plates were interchangeable, allowing for congruent and incongruent endpoint orientations when participants rotated the cubes either 45 or 90°. **(A)** shows the interchangeable target plates, **(B)** shows the position of the hands and cubes for congruent endpoint orientations, **(C)** shows target plates that require incongruent endpoint orientations of the hands and cubes, and **(D)** shows different start positions for the hands and cubes, which lead to congruent endpoint orientations despite different rotation magnitudes.

both hands in the following locations: thumb – dorsoradial aspect of the distal phalanx, index finger – dorsomedial aspect of the distal phalanx, wrist – radial aspect of the distal styloid process. LEDs were also positioned on both cubic wooden objects, which measured 4 cm × 4 cm × 4 cm. Position data from the LEDs were sampled at 200 Hz, stored, and then analyzed off-line using custom software (KinSys, Eh-Soft).

PROCEDURE

Before beginning each trial, the height of the participant's seat was adjusted so that their elbows were flexed at 90° with both forearms parallel to the floor when their hands were positioned at the start position. No other adaptations for the participant's body measurements were made (i.e., reach distance and object size was the same for all participants). They grasped one object with the right hand and one object with the left hand using a precision grip. The objects were placed on two start positions located 12 cm to right and left of the participant's midline. Participants initiated their movements on a verbal "Go" signal provided by the experimenter.

The task was to transport the two objects 30 cm from the start positions while rotating them either 45 or 90° outward (i.e., laterally) to place them into target wells (**Figures 1A,B**). Outward rotation of the blocks was demonstrated to participants, and they were instructed that all trials required a rotation movement (i.e., even when a rotation of 0° would allow them to place an object in the target, as shown for the 90° target in **Figure 1D**, they were asked to rotate the object). Target wells were the same size as the objects, resulting in a tight fit. Participants were asked to move at a comfortable pace and no instructions were given regarding the simultaneity of transport or rotation movements of the right and left hands. All trials were performed with each hand acting on the corresponding side of space (i.e., the right hand moved in right space). Participants were given three practice trials in the congruent condition prior to the beginning of data collection.

The magnitude of the rotation movements required to place the objects within the target wells could be the same (i.e., both 45 or 90°) or different (i.e., one 45 and 90°) for the two hands. Endpoint congruency (i.e., goal) was also manipulated such that the hands ended either in the same orientation (congruent; see **Figure 1B**) or in different orientations (incongruent; see **Figure 1C**). To achieve differences in endpoint congruency for the same rotation magnitude (or alternatively, congruent endpoints with different rotation magnitudes), the orientation of the object at the start position was manipulated (see **Figure 1D**). Any combination of start position and rotation magnitude that caused an outward rotation of the hand past the posture shown in **Figure 1B** was removed. Further, although more than one combination of start orientations could satisfy the incongruent L45R45 and incongruent L90R90 conditions, to maintain a balanced design we chose only one combination. While it is possible that the start orientation may have an asymmetric influence on the two hands, we feel that testing this effect is beyond the scope of the current study. The start and end orientations for both cubes in each condition are represented in **Table 1**. Light pencil outlines of the cubes for each orientation were used by the experimenter to place the object in the starting orientation for a given trial. The participant was then asked to grasp the cube at that starting orientation. The experimenter visually confirmed that the object had not been re-oriented by the participant prior to the start of the trial.

Manipulation of the rotation magnitude (45°, 90°), rotation magnitude congruency (same, different) and endpoint congruency (congruent, incongruent) factors resulted in a total of eight conditions. Each participant completed 10 trials in a blocked order for each of the conditions for a total of 80 trials[1]. The conditions were presented in a random order.

DATA ANALYSIS

Transport and rotate

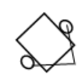
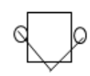
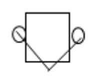
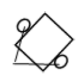
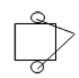
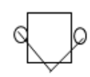
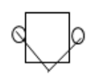
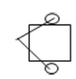
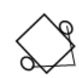
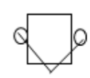
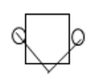
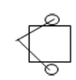
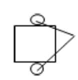
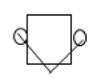
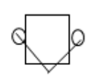
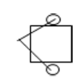
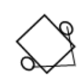
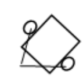
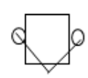
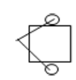
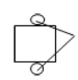
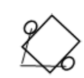
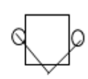
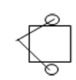
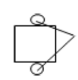
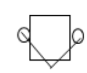
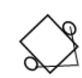
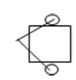
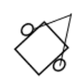
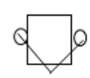
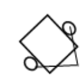
The three-dimensional position data recorded from the LEDs positioned on the index finger, thumb, and wrist of both hands were first interpolated over missing data points of no more than 20 ms and filtered using a dual-pass second order Butterworth low pass filter with a cutoff frequency of 7 Hz.

Movements were divided into two components; object transport toward the target location and rotation of the object to match the orientation of the target well. Start of object transport was defined as the point where tangential wrist velocity increased above a threshold of 5 mm/s and continued to rise. The end of object transport was determined as the time after peak velocity when the wrist velocity in the forward (x) direction first decreased below a threshold value of 5 mm/s. The main kinematic measure of interest for object transport was transport time. Rotation of the object by the hand was determined using the LEDs on the thumb and wrist. Rotation was defined as the change in the angle between the X-axis and the straight line connecting the LEDs on the wrist and thumb, with the origin passing through the wrist LED (see **Figure 2**). Note that an angle of 0 was recorded when the line connecting the wrist and thumb was parallel to the X-axis, whereas an angle of 90° was recorded when the line connecting the wrist and thumb was parallel to the Y-axis. The start of rotation was defined as the first occurrence of a rotation velocity of greater than 1° per second. End of rotation was determined as the point after the peak where rotation velocity decreased below a value of 1° per second. The main kinematic measure of interest for object rotation was rotation time.

Mean values for the 10 trials in each condition for the congruent endpoint orientations were submitted to separate 2 endpoint

[1]This experiment is a follow-up to Mason and Bryden (2007) in which we used a blocked design but did not control for endpoint congruency. To avoid adding a confounding factor which would prevent us from comparing our results to our previous work, we chose to maintain the blocked trial order. Follow up studies should test random trial orders to see whether blocking versus randomizing has an effect.

Table 1 | Starting and ending orientations for the hand/object in each of the eight conditions.

Condition			Start orientation		End orientation	
Rotation magnitude (left hand)	**Rotation magnitude (right hand)**	**Endpoint congruency**	**Left hand**	**Right hand**	**Left hand**	**Right hand**
45°	45°	Congruent				
45°	90°	Congruent				
90°	45°	Congruent				
90°	90°	Congruent				
45°	45°	Incongruent				
45°	90°	Incongruent				
90°	45°	Incongruent				
90°	90°	Incongruent				

The circles represent the position of the index finger and thumb on the object.

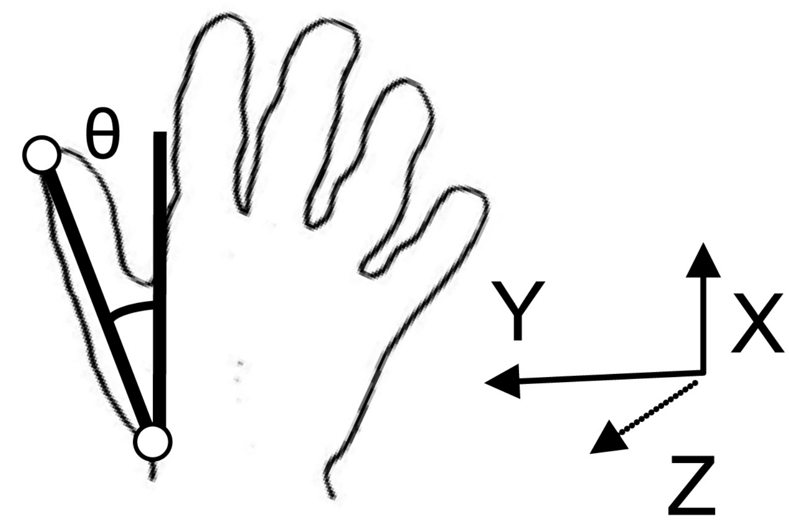


FIGURE 2 | Rotation of the object was determined using the light emitting diodes (LEDs) on the thumb and wrist. Rotation was defined as the change in the angle between the *X*-axis and the straight line connecting the LEDs on the wrist and thumb, with the origin passing through the wrist LED.

congruency (congruent, incongruent) × 2 hand (left, right) × 4 condition (L45R45, L90R90, L45R90, L90R45) repeated measures analyses of variance (ANOVA). When significant three-way interactions were found, means were compared separately for the congruent and incongruent endpoints using 2 hand (left, right) × 4 condition (L45R45, L90R90, L45R90, L90R45) repeated measures ANOVA. An *a priori* alpha level of $p < 0.05$ was used to determine significance.

Relative difference between right and left hands

To describe the temporal coordination between the movements of the two hands, we calculated relative timing differences between the left and right hands for transport start and end time and rotation start and end time. Negative values indicate that the left hand began/ended before the right hand. Means were submitted to separate 2 endpoint congruency (congruent, incongruent) × 4 condition (L45R45, L90R90, L45R90, L90R45) repeated measures ANOVA. When significant two-way interactions were found, means were compared separately for the congruent and incongruent endpoints using four condition (L45R45, L90R90, L45R90, L90R45) repeated measures ANOVA. An *a priori* alpha level of $p < 0.05$ was used to determine significance.

Relative difference between transport and rotate components: concurrency

To examine the temporal concurrency of the transport and rotation components we calculated the relative difference between start of transport and start of rotation (relative transport/rotation start time) and relative difference between end of transport and end of rotation (relative transport/rotation end time). Negative values indicate that the transport component began/ended before the rotation component. These measures were analyzed using separate 2 endpoint congruency × 2 hand (left, right) × 4 condition (L45R45, L90R90, L45R90, L90R45) repeated measures ANOVA. When significant three-way interactions were found, means were compared separately for the congruent and incongruent endpoints using 2 hand (Left, Right) × 4 condition (L45R45, L90R90, L45R90, L90R45) repeated measures ANOVA. An *a priori* alpha level of $p < 0.05$ was used to determine significance.

RESULTS

To simplify presentation and interpretation of the results, statistics for only the highest order significant interaction are presented and discussed in the text and figures below.

TRANSPORT AND ROTATE TIMES

For transport time, a significant endpoint × hand × condition interaction was found ($F_{3,33} = 9.05$, $p < 0.001$). The interaction was further decomposed by separately comparing hand and condition within the congruent and incongruent endpoint orientations. For the congruent endpoint orientations, no significant main effects or interactions were found for transport time. Overall participants took 870 ± 47 ms to transport the object from the start position to the target when endpoint orientations were congruent. When the endpoints were incongruent there was a significant interaction between condition × hand ($F_{3,33} = 15.38$, $p < 0.001$; see **Figure 3**). *Post hoc* analysis testing simple main effects of hand within condition revealed that the left hand was significantly faster than the right hand in conditions where the left hand rotated the object 45° (L45R45: $p = 0.001$; L45R90: $p = 0.009$). Differences between the right and left hands for the other two conditions (L90R90 and L90R45) were not significant.

For object rotation time a significant endpoint × hand × condition interaction was found ($F_{3,33} = 17.7$, $p < 0.001$). The interaction was further decomposed by separately comparing hand and condition within the congruent and incongruent endpoint orientations. For the congruent endpoint orientations, a significant interaction was found between condition and hand

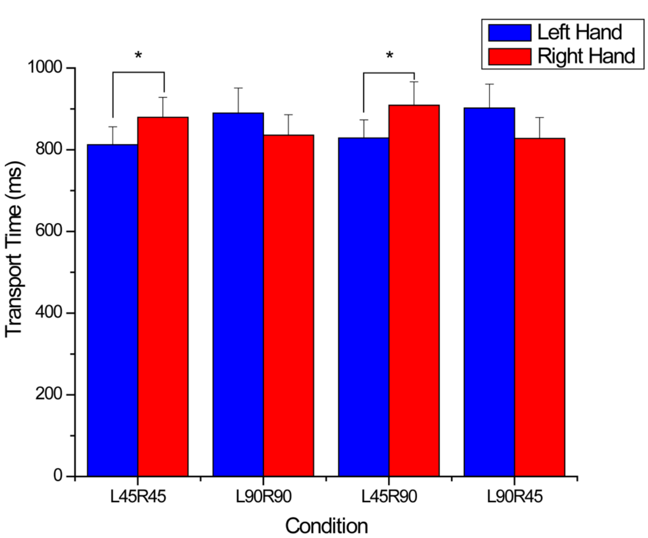


FIGURE 3 | Transport times for incongruent endpoints. For the x-axis titles, L and R refer to the left and right hands, and 45 and 90 refer to 45 and 90° rotations. Note that the left hand was significantly faster when the rotating 45°. *denotes significant ($p < 0.05$) differences between means and error bars represent SE.

($F_{3,33} = 13.4$, $p < 0.001$; see **Figure 4A**). *Post hoc* analysis testing the simple main effect of hand within condition revealed that rotation times were similar for the two hands in the L45R45 condition. When rotation magnitudes were 90° for the two hands (L90R90), rotation time was longer for the right hand ($p = 0.047$). Finally, when rotation magnitudes were different for the two hands, rotation time was longer for the hand rotating 90° (L45R90: $p = 0.014$; L90R45: $p = 0.005$).

For the incongruent endpoint orientations, a significant interaction between condition and hand ($F_{3,33} = 53.93$, $p < 0.001$) was also found. *Post hoc* analysis testing the simple main effects of hand within condition indicated that when rotation magnitudes were different, rotation time was longer for the hand rotating 90° (L45R90: $p < 0.001$; L90R45: $p < 0.001$; see **Figure 4B**). In contrast, when rotation magnitudes were the same for the two hands, rotation time was dependent on whether the two hands rotated 45 or 90°. Rotation time was longer for the right hand in the L45R45 condition ($p < 0.001$), however, when the two hands rotated 90°, rotation times were similar.

RELATIVE DIFFERENCE BETWEEN RIGHT AND LEFT HANDS: TRANSPORT AND ROTATION

No significant main effects or interactions were found for the relative timing differences between the right and left hands at the start of transport. The mean difference between the hands was -7.0 ms $\pm$ 3.6 ms regardless of endpoint congruency or condition. In contrast, an interaction between endpoint congruency and condition ($F_{3,33} = 9.0$, $p < 0.001$) was found for the end of transport. The interaction between endpoint congruency and condition was further analyzed by comparing the effect of condition for the congruent and incongruent endpoints separately. The effect of condition failed to reach significance levels for the congruent endpoint orientations. For the incongruent endpoints a main effect of condition was found ($F_{3,33}$=14.4, $p < 0.001$). *Post hoc* analysis using Fischer's LSD test indicated that the L45R45 was

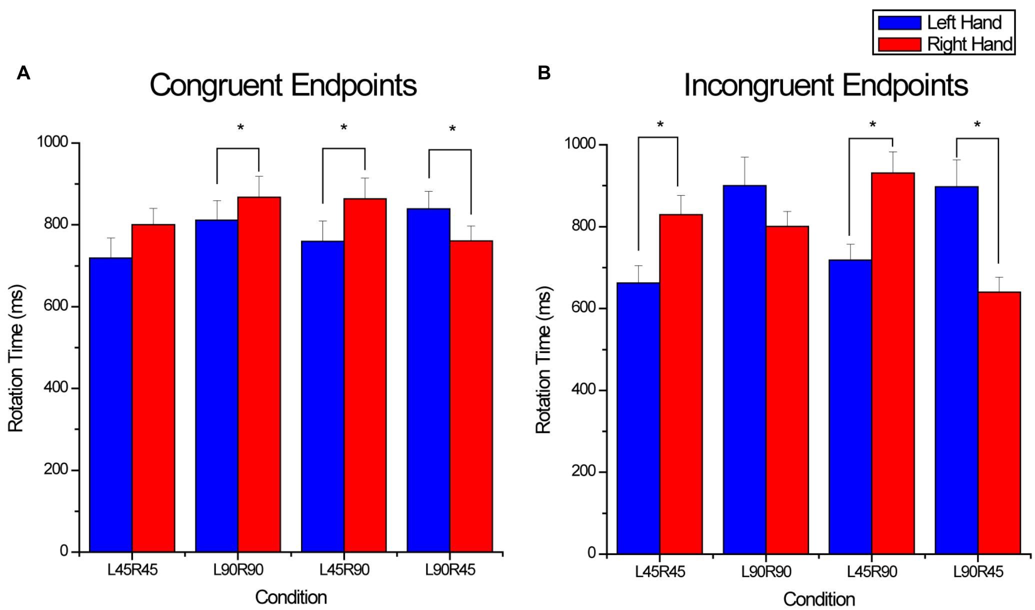


FIGURE 4 | Rotation times for the (A) congruent endpoint orientations and (B) incongruent endpoint orientations. For the x-axis titles, L and R refer to the left and right hands, and 45 and 90 refer to 45 and 90° rotations. Even when endpoint orientations were congruent and rotation magnitude was similar [e.g., L45R45 and L90R90 conditions in **(A)**], rotation times were significantly different for the two hands. *denotes significant ($p < 0.05$) differences between means and error bars represent SE.

significantly different than the L90R90 ($p = 0.003$) and the L90R45 ($p = 0.002$). Further, the L45R90 condition was significantly different than the L90R90 ($p = 0.001$) and L90R45 ($p = 0.002$) conditions. Specifically, the left hand ended transport before the right hand in conditions where the left hand rotated the object 45° (L45R45: relative difference = −72.85 ± 13.26 ms; L45R90: relative difference = −83.34 ± 23.85 ms). In contrast, the right hand ended transport before the left hand when the left hand rotated 90° (L90R90: relative difference = 45.56 ± 26.08 ms; L90R45: relative difference = 64.8 ± 33.1 ms).

For the start of rotation, an interaction between congruency and condition ($F_{3,33} = 7.3$, $p = 0.001$) was found. The interaction was further analyzed by separately comparing the effect of condition on the congruent and incongruent endpoints. The main effect of condition was significant for the start of rotation for the congruent endpoints ($F_{3,33} = 15.82$, $p < 0.001$). *Post hoc* analysis using Fischer's LSD test indicated that the L45R45 condition was significantly different than the L90R90 ($p = 0.019$), the L45R90 ($p = 0.031$) and the L90R45 ($p = 0.001$) conditions. The L90R90 was significantly different than the L45R90 ($p < 0.001$) condition. Finally, the L45R90 and L90R45 conditions were significantly different ($p < 0.001$). Results indicated that the left hand began movement before the right hand when a 90° rotation of the left hand was required (L90R90: relative difference = −31.8 ± 14.4 ms; L90R45: relative difference = −68.2 ± 22.4 ms). In contrast, the right hand began rotating before the left hand when a 45° rotation of the left hand was required (L45R45: relative difference = 33.8 ± 21.4 ms; L45R90: relative difference = 74.95 ± 16.6 ms). The main effect of condition was also significant for the incongruent endpoints ($F_{3,33} = 5.563$, $p = 0.003$). *Post hoc* analysis using Fischer's LSD test indicated that the L90R45 condition was significantly different than all other conditions (L45R45: $p = 0.03$; L90R90: $p = 0.016$; L45R90: $p < 0.001$). The left and right hands began movement approximately simultaneously for the L45R45 (Relative difference = −9.1 ± 16.9 ms), L90R90 (Relative difference = −8.11 ± 10.8 ms) and L45R90 (Relative difference = 3.57 ± 11.6 ms) conditions. In contrast, for the L90R45 condition, the left hand began movement 45.7 ± 10.8 ms before the right hand.

For the end of rotation an interaction between endpoint congruency and condition were found ($F_{3,33} = 29.9$, $p < 0.001$). The interaction was further analyzed by separately comparing the effect of condition on the congruent and incongruent endpoints. For the congruent endpoints, the main effect of condition was significant ($F_{3,33} = 5.719$, $p = 0.003$). *Post hoc* analysis using Fischer's LSD test indicated that the relative timing for the end of rotation was significantly larger in the L90R90 (−87.7 ± 25.5 ms) condition than in the L45R90 (−28.9 ± 37.8 ms, $p = 0.009$) and L90R45 (10.7 ± 27.5 ms, $p = 0.001$) conditions. The timing difference in the L45R45 was −47.7 ± 38.33 ms and did not differ significantly from any other condition. For the incongruent endpoints, a main effect of condition was also found for the relative timing at the end of rotation ($F_{3,33} = 48.615$, $p < 0.001$). *Post hoc* analysis using Fischer's LSD test indicated that the relative timing for the end of rotation was significantly different in the L45R45 condition than in the L90R90 ($p < 0.001$) and the L90R45 ($p < 0.001$) conditions. Further, relative timing at the end of rotation was significantly L45R90 conditions than in the L90R90 ($p < 0.001$) and L90R45 ($p < 0.001$). Finally, the L90R90 and L90R45 conditions were also significantly different ($p = 0.001$). Specifically, the left hand ended rotation before the right hand in conditions where the left hand rotated 45° (L45R45: relative difference = −176.3 ± 37.6 ms; L45R90: relative difference = −209.5 ± 32.51 ms). In contrast, the right hand ended rotation before the left hand in conditions where the left hand rotated 90° (L90R90: relative difference = 91.2 ± 46.73; L90R45: relative difference = 212.3 ± 49.5 ms).

RELATIVE DIFFERENCE BETWEEN TRANSPORT AND ROTATE COMPONENTS: CONCURRENCY

A significant interaction between endpoint, hand, and condition was found for the relative time difference between the start of the transport and rotation components ($F_{3,33} = 12.41$, $p < 0.001$). This interaction was further decomposed by separately comparing hand × condition for the congruent and incongruent orientations. An interaction between condition and hand was found ($F_{3,33} = 18.3$, $p < 0.001$) for relative transport/rotation start in the congruent condition (see **Figure 5A**). Simple main effects analysis comparing the left and right hands within each condition indicated that when the hands rotated different magnitudes, the hand rotating 90° began the rotation component sooner than the hand rotating 45° (L45R90: $p = 0.001$; L90R45: $p = 0.012$). For the incongruent endpoint orientations, an interaction between condition and Hand was also found ($F_{3,33} = 3.2$, $p = 0.037$) for relative transport/rotation start (see **Figure 5C**). Simple main effects analysis comparing the left and right hands for each condition indicated that the only significant difference in relative timing between the two hands was for the L90R45 condition, where the left hand began rotating sooner than the right hand ($p = 0.003$).

For the end of the movement, an interaction was found between endpoint, hand and condition ($F_{3,33} = 18.2$, $p < 0.001$). This interaction was further decomposed by separately comparing Hand and condition for the congruent and incongruent orientations. For the congruent orientations, a significant interaction between hand and condition was found ($F_{3,33} = 3.15$, $p = 0.038$; see **Figure 5B**). Simple main effects analysis comparing the left and right hands for each condition indicated that the only significant difference in relative timing between the two hands was for the L90R90 condition ($p = 0.02$). Here, the left hand ended transport approximately 30 ms after the completion of the rotation component, whereas the right hand ended rotation 60 ms after the end of transport. For the incongruent condition, an interaction was found between condition and hand ($F_{3,33} = 23.2$, $p < 0.001$). As shown in **Figure 5D**, the relative time difference between the end of transport and end of rotation was different for the two hands for all conditions except the L90R90 condition (L45R45: $p = 0.026$; L45R90: $p = 0.002$; L90R45: $p = 0.007$).

DISCUSSION

With the current study, we were interested in understanding how goal and movement congruency influenced performance in a bimanual transport, rotate, and place task that required precision at the endpoint. Previous work has indicated that for bimanual tasks, goal congruency (or end-state planning) can constrain

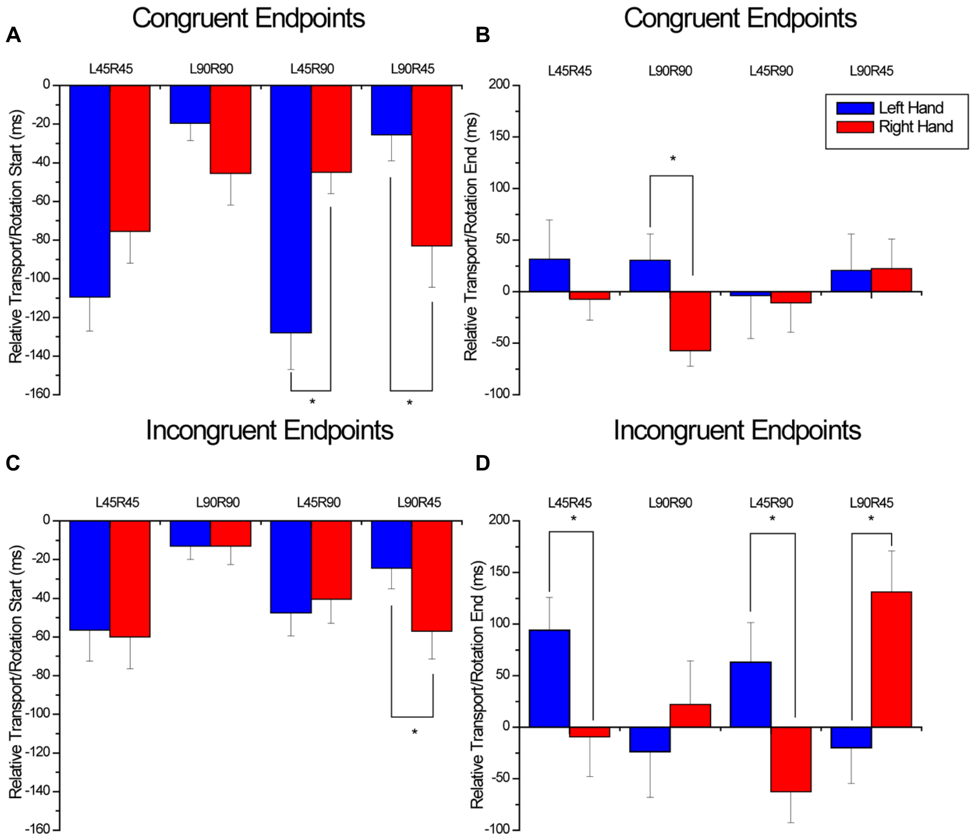


FIGURE 5 | Relative timing between the start of object transport and object rotation for the congruent (A) and incongruent (C) conditions as well as the relative timing between the end of transport and the end of rotation for the congruent (B) and incongruent (D) conditions. For the x-axis titles, L and R refer to the left and right hands, and 45 and 90 refer to 45 and 90° rotations. Overall, these four figures demonstrate an inconsistent pattern of coordination between the transport and rotation components regardless of whether the endpoints were congruent or incongruent. *denotes significant ($p < 0.05$) differences between means and error bars represent SE.

movement planning and dominate over the motor actions necessary to achieve these goals (Kunde and Weigelt, 2005; Weigelt et al., 2006). In contrast, other work has shown that movement symmetry can dominate over goal symmetry in a task dependent way (van der Wel and Rosenbaum, 2010; Huhn et al., 2014). According to Huhn et al. (2014), these previous results suggest a flexible hierarchy, where multiple constraints can take precedence depending on the task. The purpose of the current study was to determine how this flexible hierarchy would extend to tasks with increased precision requirements. Further, it was unclear from previous work whether similar constraints influence each component of a movement in a similar fashion, or whether independent effects would be seen at the component level. We analyzed the kinematic performance of the transport and rotate components separately for tasks that resulted in congruent and incongruent end-goals. The separate analysis of these two components revealed differences in the way the end-goal and movement constraints influences the planning and performance of the task.

OBJECT TRANSPORT

The results of the kinematic analysis of the object transport component revealed the strong influence of goal congruency on movement planning and execution for our task. In particular, when the required rotations for the two hands resulted in symmetric postures at the end-goal, movement times were similar for the two hands. Further relative timing differences between the hands at the start and end of movements were small (i.e., ∼6 ms) regardless of hand or condition. In contrast, for end-goals where rotations of the hands resulted in asymmetric postures, condition and hand interacted to influence movement time. These differences in movement times, which could be as large as 80 ms, resulted from synchronous start times but asynchronous end times for the two hands. These results are particularly striking when we consider the incongruent R45L45 and R90L90 conditions. In these conditions, the transport component and rotation distance remained the same for the two hands. Only the ending posture differed between the two movements. If movement symmetry was an important planning parameter in our bimanual transport and rotate task, we would have expected similar movement times and small movement asynchronies for the two hands. Thus, our results for the transport component replicate those of Kunde and Weigelt (2005) who suggested that planning and executing bimanual movements is determined by the congruency of the endpoint goal and not the coherence of the muscles used to reach the end goal.

Kunde and Weigelt (2005) proposed two potential mechanisms for the facilitatory effect of goal congruence. First, they suggested that congruent goals simplify the performance of bimanual actions because they do not require the maintenance of two separate goal postures. Second, based on the work of Diedrichsen et al. (2003), they suggested that incongruent movements require separate goals to be assigned to individual hands, which is a more difficult task than assigning the same goal to both hands. While we agree that these cognitive explanations likely account for some of the facilitatory effects of congruent goals, we would also like to suggest a third factor: sensory feedback. In particular, it has recently been shown by several research groups (including ours) that the requirement to obtain visual feedback from the two hands during the performance of slow, complex bimanual movements (i.e., reach to grasp, orientation tasks) can have a significant influence on the synchrony of movement performance (Mason and Bryden, 2007; Bingham et al., 2008; Mason and Bruyn, 2009; Srinivasan and Martin, 2010). This is in contrast to speeded, less complex aiming movements, like those used by Kelso (1995), where the fast transport times (~300 ms) reduce the time available for saccadic monitoring of both hands, thus leading to movement synchrony. In tasks like the one used in the current experiment, participants must divide their visual fixations between the two separate target locations in order to successfully achieve the task goal. Consistent with the current results, Mason and Bruyn (2009) reported an increase in the number of overt shifts in visual attention during incongruent movements when compared with congruent movements. Further, the visual feedback must be integrated with the felt position of the limbs obtained via proprioceptive feedback (Jackson et al., 2000). When participants place targets in congruent end-goal orientations, the felt and seen orientations of the two limbs should be similar when the goal orientation is achieved. This expected similarity of the afferent sensory information about the two final hand postures may provide a referent to facilitate recognition of errors at the end goal position. In contrast, when the end-goals are incongruent, visual, and proprioceptive feedback from each limb is dissimilar, resulting in an increased processing load, and no between-limb referent for determining position errors. As such, the integration of visual and proprioceptive feedback may be facilitated in tasks that require congruent end-goals for the two hands. This is necessarily independent of the similarities between the movements required to reach the end goal.

OBJECT ROTATION

In contrast to the clear determining influence of end-goal congruency on the temporal synchronization of the two limbs during object transport, end-goal appeared to play a smaller role in defining movement execution during object rotation. Even when the required rotations for the two hands resulted in symmetric postures at the end-goal, object rotation times were influenced by rotation magnitude and the hand performing the rotation (i.e., movement symmetry). Interestingly, when rotation magnitudes were similar for the two hands, rotation time was longer for the right hand than the left hand. Recently, Srinivasan and Martin (2012) reported that with practice, the left hand is prioritized as the primary hand and gaze is biased toward that hand during movement performance. Although participants in our study did not receive extended practice on our task, our results may indicate that the left hand was prioritized from the beginning due to the novelty of the task. This is supported by the results for relative timing between the hands. Specifically, the left hand began rotation prior to the right hand in half the conditions and ended prior to the right hand in all but one condition. Since our skill required precision at the endpoint, and our participants were all right-handed, they may have biased their fixations toward the left hand, only switching fixation to the right hand at the end of the movement. Thus rotations of the object in the right hand necessarily took longer to complete. Unfortunately we cannot definitively confirm this hypothesis since we did not measure eye movements. Additional work will need to be completed to determine whether prioritizing of the left hand was in fact a contributor to the asynchronies noted for rotation time.

Finally, we feel it is import to highlight the results of the analysis of concurrency of the transport and rotate components as a potential metric for inferring some of the planning processes that are employed as participants perform tasks with multiple components. **Figures 5A,B** illustrate the relative timing differences between the transport and rotate components for the congruent end-goals. **Figures 5C,D** represent the incongruent end-goals. What is interesting to note are the differences in the relative timings between the hands, particularly for the congruent conditions (see **Figures 5A,B**). These within condition/between hand differences highlight the fact that despite consistent hand transport performance, the performance of the object rotation component was highly asynchronous within the context of hand transport even with end-goal congruency. Specifically, note how the two hands start the rotation component at similar times with respect to the transport component for the congruent rotation conditions, but end the rotation component at completely different times. In fact, for the L90R90 condition, the left hand ends rotation prior to the end of transport, whereas the right hand ends after the end of transport. This suggests that at the planning level, end-goal congruency can be incorporated into the movement plan for the transport component, but for the rotation component, the plan must include necessary flexibility for the assessment of sensory feedback at the end of the task.

In sum, our results support the recent conclusions of Huhn et al. (2014) that constraints do not exert their influence on movement planning and performance in a winner take all fashion. Instead we have shown in the current work that they are integrated in a flexible fashion to exert differential influence on each component of the movement. In particular, we found that goal-congruency had a strong determining influence on the symmetry of hand transport to the target location. In contrast, the execution of the object rotation component was determined by a combination of end goal congruency and movement symmetry. The execution of each component may have also been influenced by the need to integrate visual and proprioceptive information for goal achievement.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 03 October 2014; accepted: 16 January 2015; published online: 10 February 2015.

*Citation: Mason AH and Bryden PJ (2015) The effect of endpoint congruency on bimanual transport and rotation tasks. Front. Psychol. **6**:92. doi: 10.3389/fpsyg.2015.00092*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 14 January 2015
doi: 10.3389/fpsyg.2014.01556

Handedness throughout the lifespan: cross-sectional view on sex differences as asymmetries change

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Manual asymmetries has been studied by many researchers, however contradictory findings still exist as to whether preferred manual asymmetries increases with age or do we become more ambidextrous. Recently it was shown that perhaps there is a third option, that there is no increase or decrease in laterality but rather preferred manual asymmetries remains consistent throughout adulthood. Another related finding is that females appear to have an advantage in some handedness tasks, such as the Grooved Pegboard. When a larger pegboard is used, sex differences may reverse as males may perform better when larger pegs and a larger trajectory are required. However, it is not fully understood if these sex differences arise from an early age and continue throughout life. Therefore, we sought to explore sex differences in preferred hand dominance throughout the lifespan. In order to explore preferred hand dominance during the lifespan we examined 76 children (19.4–5 year olds, 12 female, $M_{age} = 4.73$; 34.6–8 year olds, 12 female, $M_{age} = 6.97$; 23.9–12 year olds, 14 female, $M_{age} = 10.83$) in Experiment 1 and 35 healthy young right-handed adults (15 female, $M_{age} = 20.91$) and 37 healthy older right-handed adults (20 female, $M_{age} = 72.3$) in Experiment 2. Individuals were tested using a standard size (small) and modified Grooved Pegboard (larger pegboard). Our study demonstrates that hand asymmetries are present early in life (children 4–5 years old) at that these differences attenuate as a function of age until adulthood (Experiment 1). Furthermore, our results demonstrate that as we age (Experiment 2), asymmetries may increase (small and large pegboards), decrease (Annett), or stay the same (finger tapping). As well we demonstrated that the sex differences could not be entirely accounted for by hand size. Therefore, asymmetries as regard to the aging process, seems to be task specific which may account for the conflicting findings in research.

Keywords: lifespan, handedness, manual asymmetries, pegboard, sex differences

INTRODUCTION

Manual asymmetries are the differences in performance abilities between the preferred and non-preferred hand (Corey et al., 2001). One of the leading hypotheses is that manual asymmetries exist because of an individual's continued reliance on their preferred hand throughout their lifespan (Peters, 1976; Provins, 1997). For example, approximately 90% of the adult population prefers to use their preferred hand for a myriad of everyday tasks, such as writing, holding a cup, brushing their teeth, and other one-handed manual tasks (Brown et al., 2006). However, the progression and direction of hand preference varies as a person ages: children aged 3 and under are considered "mixed-handed"; adolescent (10–12 years of age) individuals seemingly preferring to exclusively use their dominant hand for various tasks (Gesell and Ames, 1947; Ittyerah, 2013; Gooderham and Bryden, 2014); while adults appear to rely less on the preferred hand (Gooderham and Bryden, 2014). Furthermore, there have been conflicting findings as to whether asymmetries increase (e.g., Weller and Latimer-Sayer, 1985), decline (e.g., Kalisch et al., 2006), or remain constant (e.g., Chua et al., 1995; Francis and Spirduso, 2000; Cabeza, 2002; Hausmann et al., 2003; Przybyla and Sainburg, 2010) throughout the rest of our lives. Therefore, this study endeavors to provide an examination of the changes in the strength of manual asymmetries throughout the lifespan by comparing children, adults, and older adults. Secondly this study investigates how sex differences may impact manual asymmetries.

One method of determining laterality throughout the lifespan is to compare hand preference and performance of children, adults, and older adults. A study conducted by Carlier et al. (2006) on children aged 3–10 clearly demonstrates an increased reliance on the preferred hand as a function of age. In this study cards were placed in a semi-circle in front of the participant; with three cards being placed on the right side and three on the left. The authors noticed that younger children aged 3–4 reached across their body/midline to grasp the cards less often than children aged 7 and above. Reaching across the midline is considered a less efficient biomechanical movement as the hand has to travel further compared to using the hand on the same side, which also demonstrates an individual's reliance on their preferred hand to accomplish various tasks. Therefore, the number of children reaching with their preferred hand (right hand) to grasp cards on their left side increased with age, suggesting that younger children (aged 3–4) may produce more biomechanically efficient movements or are less dependent on their preferred hand (Carlier et al., 2006). At an older age biomechanical efficiency is seemingly replaced with hand preference, as children aged 8–10 prefer to rely on their preferred hand for reaching (Gesell and Ames, 1947; McManus et al., 1988; Carlier et al., 2006; Ittyerah, 2013).

Therefore, hand preference seems to increase and perhaps peak around 8–10 years old (Carlier et al., 2006), with preferential hand reaching across the midline decreasing in adulthood (e.g., Bryden and Roy, 2006). However, research regarding how we progressively age after adulthood demonstrates conflicting findings regarding changes in manual asymmetries. There exist at least two partially conflicting models that endeavor to explain the direction and degree of manual asymmetries with respect to aging (Weller and Latimer-Sayer, 1985; Cabeza, 2002; Hausmann et al., 2003) with one hypothesis based on the hemi-aging model. The hemi-aging model states that the advantage seen for the preferred hand's performance would become more pronounced, with a person essentially reverting back to their performance during adolescent years (Brown and Jaffe, 1975; Weller and Latimer-Sayer, 1985; Albert, 1988). Evidence for the hemi-aging model is based on the decline in performance IQ (Wechsler Adult Intelligence Scale) of older adults (Goldstien and Shelley, 1981), which incorporates subtests that have a speed component (unlike the verbal IQ). These findings formed the crux of hemi-aging model and indicated that the right hemisphere aged more rapidly than the left and also suggested a more rapid decline in left hand motor performance (Meudell and Greenhalgh, 1987). To test this hypothesis, Weller and Latimer-Sayer (1985) used a standardized Grooved Pegboard (Federal Security Agency, 1949), which is a visuomotor task that measures motor performance of both hands. They found that abilities typically associated with the right hemisphere were affected more by aging and that the motor performance of the left hand, which is controlled by the right hemisphere, declined to a greater degree than the right hand (Weller and Latimer-Sayer, 1985).

Although the hemi-aging model was quite popular, more recently research has produced an alternative view. The second hypothesis is called the hemispheric asymmetry reduction in older adults, or HAROLD Model and is based on the results of functional neuroimaging of patterns of activation during cognitive and motor tasks in younger and older adults (Cabeza, 2001). Previous research utilizing unimanual motor tasks like finger tapping and hand grip task (grasping at percentage of peak grip strength) have revealed a more symmetric hemispheric activation (Mattay et al., 2002; Ward and Frackowiak, 2003; Rowe et al., 2006). A study employing a unimanual reaching task involving older adults (60–80 years old) discovered that there were smaller asymmetries in motor performance between the left and right hands of older adults compared to younger adults (Przybyla et al., 2011). Furthermore, results revealed that older adults using their non-preferred hand generated straighter trajectories (suggests an efficient movement) much like their preferred hand, compared to younger adults who tended to have larger hand path curvatures (suggests less efficient movement) when using their non-preferred hand (Przybyla et al., 2011). Additionally, there were no differences in accuracy between the preferred and non-preferred hand in older adults, but younger adults were more accurate with their preferred hand (Przybyla et al., 2011). A more contemporary hypothesis, similar to the conclusions of the HAROLD model is based on use dependent plasticity and states that as individuals age the performance and ability of the preferred hand will decrease, relative to its non-preferred counterpart simply because of an inactive lifestyle and less usage (Kalisch et al., 2006). The result of a more sedentary lifestyle and underutilization of the preferred hand made the performance differences between the preferred and non-preferred hand less pronounced as individuals aged and resulted in an overall decrease in asymmetries (Kalisch et al., 2006). It should be noted that unlike the HAROLD model where the motor performance of the non-preferred hand improves, this model demonstrates a decline in the performance of the preferred hand as demonstrated using task such as line tracing, aiming, and tapping (Kalisch et al., 2006).

Although aging is an important factor that impacts hand performance, Bornstein (1985) have also demonstrated that females were consistently faster than men on Grooved Pegboard tests, with other researchers replicating these findings (e.g., Ruff and Parker, 1993; Schmidt et al., 2000; Bryden and Roy, 2006). Despite the various studies demonstrating that women perform better than men on the Grooved Pegboard task, there is still a limited understanding as to why this occurs. Researchers have noticed that both men and women with larger fingers had trouble grasping the pegs, which would have negatively affected (i.e., slow down) performance (Peters et al., 1990). Peters et al. (1990) demonstrated that differences in performance between men and women dissipated once finger size was accounted for. To further explore the role of finger size Peters and Campagnaro's (1996) subsequent study had their participants use tweezers to manipulate the pegs and discovered that the performance differences between sexes were negligible. This hypothesis is also supported by the findings of Kilshaw and Annett (1983) as using a larger pegboard revealed no or little differences between the sexes. Therefore, the role of sex differences should be investigated across the lifespan.

Therefore, the purpose of these studies was to examine how the direction and degree or strength of manual asymmetries are affected as a function of age in performance measures (i.e., movement time) and how sex plays a role. We hypothesized that since youngest children would be mixed handed, the performance measures between the hands would not be different. As the age of the participants increased, so would the reliance on the preferred hand and therefore performance with the preferred hand would be better as it is used more. However, the reliance on the preferred hand would decrease once adults were tested (see Gooderham and Bryden, 2014), and performance differences would decrease for older adults, as they would revert to a childhood handedness pattern. Regarding sex, we predict that females will perform better than males, and these differences will dissipate after hand size is accounted.

EXPERIMENT 1

We sought to explore how sex differences may impact asymmetries during the childhood ages by manipulating the size of the pegboards utilized, as well as the corresponding peg size. The specific hypotheses for Experiment 1 were that we would see an interaction between the hand used and age group, and that sex differences would disappear when using the larger pegboard. Specifically, we believed that the youngest children would show smaller differences in performance between preferred and non-preferred hands due to the constant usage of both hands in everyday tasks. Furthermore, children aged 10–12 would demonstrate the largest difference between hand performance, as they tend to rely on their preferred hand (Carlier et al., 2006; Rezaee et al., 2010; Gooderham and Bryden, 2014). We hypothesized that adults would have smaller differences between the hands compared to the children aged 10–12. We also hypothesized that these findings would be seen irrespective of the task used. Thirdly we hypothesized that females would perform better than males (see Peters and Campagnaro's, 1996), but only for the smaller pegboard. Sex differences would disappear when the larger pegboard is used (Kilshaw and Annett, 1983).

MATERIALS AND METHODS

Participants

A total of 76 healthy right-handed children were tested (19.4–5 year olds, 12 female, $M_{\text{age}} = 4.73$, $SD = 0.5$; 34.6–8 year olds, 12 female, $M_{\text{age}} = 6.97$, $SD = 0.9$; 23.9–12 year olds, 14 female, $M_{\text{age}} = 10.83$, $SD = 1$) and 36 healthy young right-handed adults (20 females $M_{\text{age}} = 21.31$, $SD = 1$). The handedness of the participants was determined utilizing the Waterloo Handedness Questionnaire. Prior to starting the study all participants were informed of the protocols and written consent was obtained. This study was approved by the Office of Research Ethics at Wilfrid Laurier University. One limitation of the study was that we were not able to obtain WHQ scores for some of the children due to their age as they may not fully understand the questions asked and may not provide reliable results.

Apparatus

The 22-item Waterloo Handedness Questionnaire (see Cavill and Bryden, 2003) was used to determine hand preference for the adults only. This study used two different types of pegboards: (1) The Lafayette Instrument (Model #32025) standard Grooved Pegboard, which will be referred to as the small pegboard from now on (see Ruff and Parker, 1993; Bryden and Roy, 2006); (2) Modified Grooved Pegboard, which will be referred to as the large pegboard from now on. The small pegboard has a 10.1 cm by 10.1 cm metal surface with 5 rows and 5 columns of grooved holes. The holes were aligned in a manner in which the peg must be carefully oriented in order to place the peg into the hole. All the holes were aligned in a different manner. Each participant was required to place 25 pegs (3.0 mm in diameter and 2.5 cm in length) into the receptacles. The large Grooved Pegboard is based on the design of the small pegboard and built to be approximately 2 times the size of the small pegboard. This pegboard has a 20.5 cm by 20.5 cm metal surface with five rows of 5 keyhole shaped holes with a receptacle at the bottom. The holes in this pegboard are positioned in the same way as the small pegboard. The pegs for this pegboard were scaled to a bigger size with a diameter of 9 and 70 mm in length.

Procedure

After acquiring informed written consent and determining handedness, the participants' thumbs and index fingers were measured. Participants were then asked to complete the two aforementioned pegboard tasks (small and large), in a randomized schedule. The Pegboard tasks require the participant to perform two different phases: place and replace; however for the purposes of this paper we will only focus on the place time. During the place phase, participants were asked to place pegs into their respective holes. For example, the participants were instructed to remove the pegs from the receptacle and place them in the grooves, starting on the side opposite to the hand placing the pegs. If the participant was starting with their right hand they would start on the left side and move to the right; whereas the left hand had the mirror image (started on the right side and move left).

Finally the participants were instructed to perform the task as quickly as possible. Timing commenced once the first peg was grasped and a total of three trials were performed by each hand for each of the pegboards.

Data reduction

Average movement time was calculated for each of the pegboards for all the groups. However, the data was not normally distributed; therefore a log base 10 transformation was applied for statistical analysis. The transformed data minimize the number of violations for statistical analysis (with the exception of the youngest children); therefore the transformed data was analyzed. The data was then transformed back for the purposes of presentation.

Waterloo handedness questionnaire. The questionnaire serves as self-report measure of hand preference, as participants were asked to indicate their preferred hand for 22-unimanual tasks (Steenhuis and Bryden, 1989). Each question permits five responses: "left always" (−2), "left usually" (−1), "uses both hands equally often" (0), "right usually" (+1), and "right always" (+2), thus enabling an overall handedness score to be computed by summing the responses. As expected participants averaged a positive score (adult females $M = 31.6$, $SD = 5.6$; adult males $M = 28.9$, $SD = 3.9$).

Data analysis

Place time for the children and adults was submitted to a 3 Group (younger children, older children, adults) × 2 Sex (male, female) × 2 Pegboards (small, large) × 2 Hand (left, right) mixed ANOVA with the last two factors as repeated measures. Any violations to the assumptions of normality were corrected using a Greenhouse-Geisser correction. *Post-hoc* analyses using Tukey HSD were used to examine any effects involving more than two means.

RESULTS

All main effects and interactions that were not of interest are presented in **Table 1**. A significant Sex × Pegboard interaction, $F_{(1, 104)} = 8.4$, $p < 0.01$, $\eta^2 = 0.08$ was revealed. The *post-hoc*

Table 1 | Means and standard errors (in brackets) for main effects and interactions for both Experiments for all the variables (V).

Exp	Effect	V1	V2	V3	V4
1					
	Group $F_{(3, 104)} = 82.97$, $p < 0.001$, $\eta^2 = 0.71$	4–5 95.7 s (1.04 s)	6–8 73.1 s (1.03 s)	9–12 54.5 s (1 s)	Adults 49.6 s (1 s)
	Pegboard $F_{(1, 104)} = 223.87$, $p < 0.001$, $\eta^2 = 0.68$	Small 71.5 s (1.02 s)	Large 60.8 s (1.02 s)	N/A	N/A
	Hand $F_{(1, 104)} = 172.24$, $p < 0.001$, $\eta^2 = 0.62$	P 61.4 s (1.01 s)	NP 70.8 s (1.02 s)	N/A	N/A
	Group × Pegboard $F_{(3, 104)} = 14.1$, $p < 0.001$, $\eta^2 = 0.29$	4–5 year olds	6–8 year olds	9–12 year olds	Adults
	Small Pegboard	103.99 s (1.04 s)	77.8 s (1.03 s)	57.02 s (1.04 s)	56.36 s (1.03 s)
	Large Pegboard	87.9 s (1.04 s)	68.87 s (1.03 s)	52 s (1.03 s)	43.45 s (1.03 s)
	Group × Hand $F_{(3, 104)} = 5.71$, $p < 0.001$, $\eta^2 = 0.62$	4–5 year olds	6–8 year olds	9–12 year olds	Adults
	Preferred	87.3 s (1.04 s)	67.14 s (1.03 s)	50.58 s (1.04 s)	47.64 s (1.03 s)
	Non-Preferred	104.71 s (1.5 s)	79.8 s (1.03 s)	58.62 s (1.04 s)	51.4 s (1.03 s)
2					
Pegboards	Group $F_{(1, 65)} = 62.82$, $p < 0.001$, $\eta^2 = 0.49$	YA 53.7 s (1.96 s)	OA 76 s (1.89 s)	N/A	N/A
	Pegboard $F_{(1,65)}$=246.24, $p < 0.001$, $\eta^2 = 0.79$	Small 73.3 s (1.77 s)	Large 56.4 s (0.95)	N/A	N/A
	Hand $F_{(1, 65)} = 62.43$, $p < 0.001$, η^2= 0.49	P 61.5 s (1.15 s)	NP 68.2 s (1.58 s)	N/A	N/A
	Hand × Pegboard $F_{(1, 65)} = 14.44$ $p < 0.001$, $\eta^2 = 0.18$	Small	Large		
	Preferred	68.94 s (1.49 s)	54.05 s (0.93 s)		
	Non-Preferred	77.58 s (2.18 s)	58.82 s (1.09 s)		
Annett	Group $F_{(1,65)}$ =61.9, $p < 0.001$, $\eta^2 = 0.49$	YA 10.5 s (1.02 s)	OA 13.6 s (1.02 s)	N/A	N/A
	Hand $F_{(1, 65)} = 29.04$, $p < 0.001$, $\eta^2 = 0.31$	P 11.6 s (1.02 s)	NP 12.4 s (1.95 s)	N/A	N/A
Tapping	Group $F_{(1, 65)}$ =6.93, $p = 0.011$, $\eta^2 = 0.1$	YA 48.48 taps (1.5 taps)	OA 42.84 taps (1.44 taps)	N/A	N/A

(Continued)

Table 1 | Continued

Exp	Effect	V1	V2	V3	V4
	Sex $F_{(1, 65)} = 5.42$, $p = 0.023$, $\eta^2 = 0.08$	F 43.21 taps (1.5 taps)	M 48.12 taps (1.4 taps)	N/A	N/A
	Hand $F_{(1, 65)} = 13.9$, $p < 0.001$, $\eta^2 = 0.18$	P 46.82 taps (1.11 taps)	NP 44.5 taps (0.98 taps)	N/A	N/A

Variables are represented by the following abbreviations: P, Preferred Hand; NP, Non-Preferred Hand; YA, Younger Adults; OA, Older Adults; F, Females; and M, Males.

analysis, however, revealed that both females and males were better at the large pegboard (62.09 s, $SE = 1.02$ s and 59.43 s, $SE = 1.02$ s respectively) compared to the small pegboard (70.79 s, $SE = 1.03$ and 72.11 s, $SE = 1.03$ s respectively). However, *post-hoc* analysis did not reveal any differences between sexes on either pegboard.

A Group × Hand × Pegboard, $F_{(3, 104)} = 3.03$, $p = 0.033$, $\eta^2 = 0.08$ was also revealed. Overall the youngest children (4–5) were slower compared to all other groups, regardless of hand used or pegboard size. The next slowest group was the 6–8 year olds, also showing hand differences regardless of pegboard size, and the 9–12 year olds and adults behaved similarly (see **Figure 1**). To further explain the trends, place time decreased as the age of the participants tested increased regardless of which pegboard size was used. Furthermore, asymmetries decreased as a function of age with the adults having little to no difference in how the preferred and non-preferred hands performed. Lastly, the youngest age group and the adults demonstrated faster place times when using both the small and large pegboards; however the 6–8 and the 9–12 year olds did not show a difference between the small and large pegboards when using their preferred hands (see **Figure 1**).

DISCUSSION

The results confirm one of our hypotheses, as the youngest children (4–5) were slower to complete the tasks (i.e., both pegboards) compared to older children (9–12). These findings are in line with previous findings of childhood performances (e.g., Gesell and Ames, 1947; Gooderham and Bryden, 2014). As well our findings demonstrate that the adults are least lateralized, as there were no statistical differences when comparing the preferred or non-preferred hands on both the Grooved Pegboard and larger pegboard tasks, which may be explained by previous findings on laterality. Researchers have proposed that as we age into our adult years, we have a reduced dependency on our preferred hand and rely more on biomechanical efficiency (Bishop et al., 1996; Bryden and Roy, 2006; Bryden et al., 2011; Gooderham and Bryden, 2014). However, it should be noted when the data for the adults are analyzed separately (not included in analysis with the data from the children; $F_{(1, 34)} = 27.38$, $p < 0.001$, $\eta^2 = 0.45$ for main effect of Hand when adults are analyzed separately) the results demonstrate a difference between hands, therefore this suggests that the variability introduced by the other groups washes these differences out. Therefore, it can be said that the differences seen in the youngest participants, and the 6–8 year olds show a big performance difference between the hands, and these differences may attenuate as we age (as seen as gradual disappearance in hand difference until reach adulthood).

Our second hypothesis was generally supported as the youngest group performed the slowest regardless of which task was used. However, our finding suggest that children aged 9–12 behave more like adults and do not show performance difference between the hands contradictory to previous studies (Carlier et al., 2006; Rezaee et al., 2010; Gooderham and Bryden, 2014). It is important to note that we measured actual relative hand performance in movement time as opposed to preferred hand reaching used in these other studies, which may account for the difference in findings.

Lastly our hypothesis that sex differences would only be observed for the small pegboard was not supported. Instead no sex differences were found which we postulate may be related to the large differences in body sizes across children. That is, children are still growing therefore some hands for females may be bigger than males and vice-versa which may wash out any differences. In the future, it may be prudent to take more objective measures to account for hand size, such as the work by Peters et al. (1990), instead of having indirect measures, such as varying sizes of the pegboards, to account for hand sizes. Therefore, further exploration is warranted to determine if using the small and large pegboards would support previous findings when using older adults and if sex differences emerge after childhood. Therefore, the purpose of Experiment 2 was to further explore the aging process and determine whether or not manual asymmetries fluctuate.

EXPERIMENT 2

For Experiment 2 we sought to further explore the aging process by examining how asymmetries may be affected past adulthood. As well, given that we failed to find any sex differences in Experiment 1, which we postulate might be related to differences in growth rates for males and females, we sought to explore the role of sex differences in manual asymmetries in adults and older adults in addition to further exploring the role of hand size. To explore hand size, we measured the size of the fingers in a similar fashion that used by Peters and colleagues (e.g., Peters et al., 1990; Peters and Campagnaro, 1996).

The specific hypothesis for Experiment 2 was that we would observe a Group by Hand interaction as the older group would revert back to child-like patterns of behavior, in that the difference between the performance of the preferred and non-preferred hands

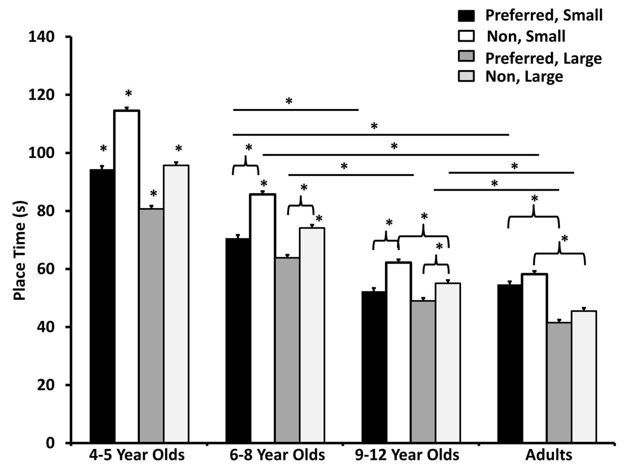

FIGURE 1 | Time taken to place all the pegs for all the groups using preferred and non-preferred hands. Stars denote significant different from all others (no lines) or when directly compared to other conditions within a group (brackets) or between groups (lines).

would decrease compared to the younger adults. The second hypothesis is that sex differences would disappear once finger size was used as a covariate and when the larger pegboard is used (see Peters et al., 1990) and when the large pegboard is used (Kilshaw and Annett, 1983). As well other measures of hand performance were used to determine if the findings of the small and large pegboard are task specific or can be generalized to other tasks such as the Annett Pegboard, peak grip strength, and finger tapping.

MATERIALS AND METHODS

Participants

A total of 35 healthy young right-handed adults (15 female, $M_{age} = 20.91, SD = 2.4$) and 37 healthy older right-handed adults (20 female, $M_{age} = 72.3, SD = 7.96$) were tested. Prior to starting the study all participants were informed of the protocols and written consent was obtained. This study was approved by the Office of Research Ethics at the University of Waterloo.

Apparatus

The Waterloo Handedness Questionnaire (see Steenhuis and Bryden, 1989) was used to determine hand preference. This study used the same apparatus as in Experiment 1 with the addition of the Annett Pegboard, a dynamometer to measure grip strength, and a finger tapper to measure fine motor control as reflected in the number of taps.

Procedure

The same procedure as Experiment 1 was used, with the addition of the Annett pegboard in which participants moved the 10 pegs from the top row to the bottom row starting on the contralateral side. Upon completing the pegboard tasks participants utilized a hand dynamometer to measure peak grip strength (N) for each hand. Each participant utilized the dynamometer with each hand 3 times. Lastly, the participants had to perform a finger tapping task, where performance was measured by how many times a participant could tap a button in 10 s. Each participant performed the finger tapping (Lafayette) task 3 times with each hand. The order of tasks was randomized between participants.

Data reduction

Average movement time was calculated for the separate pegboard tasks, for the place component for each hand. As well the average grip strength was calculated for each hand, and the average number of taps for a 10 s period. For the Annett pegboard, the data was not normally distributed and therefore a log base 10 transformation was applied before statistical analysis and interpretation. The data was transformed back for the purposes of the presentation of results (i.e., following interpretation).

Covariate analysis. Finger size for the index finger and thumb were measured and summated in the same manner as Peters et al. (1990). However, instead of using separate covariates for the left and right hand measurements, principle component analysis was used to determine a representative covariate as the sizes of the fingers in both hands were highly correlated to each other ($r = 0.91$).

Waterloo handedness questionnaire. Here, participants were asked to indicate their preferred hand for 32-unimanual tasks (Steenhuis and Bryden, 1989). Each question permits five responses: "left always" (−2), "left usually" (−1), "uses both hands equally often" (0), "right usually" (+1), and "right always" (+2), thus enabling an overall handedness score to be computed by summing the responses. As expected participants average a positive score (younger females $M = 46.87$, $SD = 8.3$; younger males $M = 40.3, SD = 13.85$; older females $M = 45.5, SD = 12.1$; older males $M = 46.8$, $SD = 9.9$).

Data analysis

Place time for the small pegboard and large pegboard was submitted to a 2 Group (younger, older) × 2 Sex (female, male) × 2 Hand (left, right) × 2 Pegboard (small, large) mixed ANOVA, with the last two factors as repeated measures. Movement times for the Annett Pegboard, finger tapping, and hand grip strength were all analyzed separately in a 2 Group (younger, older) × 2 Sex (female, male) × 2 Hand (left, right) mixed ANOVA. Any violations to the assumptions of normality were corrected using a Greenhouse-Geisser correction. Any effects involving more than two means was *post-hoc* tested using Tukey HSD.

RESULTS

All main effects and interactions that were not of interest are presented in **Table 1**. Results are presented with hand size used as covariate with results prior to hand size being used as a covariate presented at the bottom of each section if there were any.

Small and large pegboard

There was a Group x Pegboard, $F_{(1, 65)} = 19.22, p < 0.001, \eta^2 = 0.23$ interaction both younger and older adults are faster to complete the large pegboard (47.79 s, $SE = 1.43$ and 65.08 s, $SE = 1.37$ s respectively) compared to the small pegboard (59.75 s, $SE = 2.64$ and 86.95 s, $SE = 2.54$ s respectively). In addition, the younger adults were faster compared to the older adults on both the small and large pegboards.

A Sex × Pegboard, $F_{(1, 65)} = 7.982, p = 0.006, \eta^2 = 0.11$ interaction was revealed. Females were faster at completing the small pegboard (69.41 s, $SE = 2.62$ s) compared to the males (77.11 s, $SE = 2.52$ s). However, there was no difference when comparing the large pegboard between sexes (55.78 s, $SE = 1.41$ s for females and 57.09 s, $SE = 1.36$ s for males).

Finally the interaction of interest was the Group × Hand, $F_{(1, 65)} = 11.63$, $p = 0.001$, $\eta^2 = 0.15$ interaction. There were no differences in the time to complete the tasks in the younger adults when comparing the preferred and non-preferred hands. However, the older adults took significantly longer to perform the tasks with the non-preferred hand (see **Figure 2**).

Analysis prior to using finger size as a covariate revealed a main effect for Sex ($p = 0.023$). The finding was that females (62.59 s, $SE = 1.95$ s) were slightly faster than males (67.1 s, $SE =$ 1.87 s).However, after using finger size as a covariate, the main effect for Sex disappeared ($p = 0.109$).

Annett pegboard

A Hand × Group, $F_{(1, 65)} = 5.38$, $p = 0.024$, $\eta^2 = 0.08$ was revealed. *Post-hoc* analysis showed that older adults did not show a difference between preferred (13.34 s, $SE = 1.02$ s) and non-preferred (13.8 s, $SE = 1.02$ s) hands. However, younger adults showed faster completion times with the preferred (10.05 s, $SE =$ 1.02 s) compared to non-preferred (11.07 s, $SE = 1.03$ s) hand.

Grip strength

Only main effects were found for grip strength. A main effect for Group, $F_{(1, 65)} = 52.61$, $p < 0.001$, $\eta^2 = 0.45$ was found, as the younger adults had a higher peak grip strength (36.2N, $SE = 1.01$N) compared to the older adults (25.7N, $SE = 0.97$N). There was also a main effect for Sex, $F_{(1, 65)} = 52.16$, $p < 0.001$, $\eta^2 = 0.45$ was revealed. Males (36.1N, $SE = 0.97$N) had higher peak grip strength compared to females (25.8N, $SE = 1$N). Lastly a main effect for Hand, $F_{(1, 65)} = 31.55$, $p < 0.001$, $\eta^2 = 0.33$, was revealed as the preferred hand (32.2N, $SE = 0.71$N) had higher peak grip strength compared to the non-preferred hand (29.7N, $SE = 0.71$N).

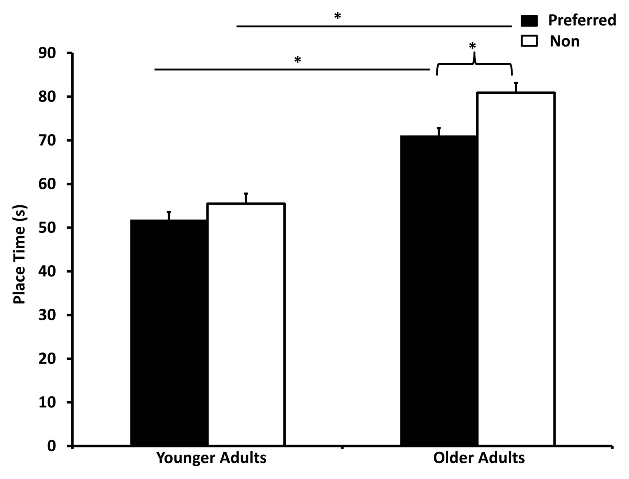

FIGURE 2 | Time taken to place the pegs using the preferred and non-preferred hands for both younger and older adults. Between group comparisons are made using lines, and within group comparisons are made using brackets. Stars denote significant differences.

Finger tapping

A Hand × Group × Sex, $F_{(1, 65)} = 4.55$, $p = 0.037$, $\eta^2 = 0.07$ was found. When *post-hoc* analysis was done, younger males (51 taps, $SE = 1.9$ taps) were able to tap more than younger females (43.47 taps, $SE = 2.1$ taps) when using their preferred hand. However, when using their non-preferred hands younger males and females did not differ (50.76 taps, $SE = 2.1$ taps and 48.07 taps, $SE = 2.37$ taps respectively). In addition younger males were able to tap more with their preferred hands compared to older males using their preferred hands (43.68 taps, $SE = 2.11$ taps) but did not differ when comparing their non-preferred hands (46.95 taps, $SE = 2.4$ taps). For females, the opposite was true as the younger adults were able to tap more with their non-preferred hands compared to the older females (41.53 taps, $SE = 2.1$ taps) but not when comparing the preferred hands (39.2 taps, $SE = 1.9$ taps for older females). The older adults did not differ when comparing preferred or non-preferred hands or sexes.

DISCUSSION

When aging is further explored when using the Grooved pegboards, it seems that manual asymmetries increase as a function of aging, which supports the hemi-aging model. Younger adults again did not show any differences but the older adults demonstrated better performance using the preferred hand. However, the findings of the Annett Pegboard support a decrease in manual asymmetries, or the HAROLD model or the use dependent plasticity model. Our findings cannot determine whether the motor performance of the non-preferred hand improved or the performance of the preferred hand declined for the older participants, instead future research may need to conducted with a longitudinal design rather than cross-sectional. Furthermore, finger tapping revealed that younger males were able to tap more than females when using their preferred hands and that older adults did not show any sex or hand differences. Therefore, it seems that our findings suggest a degree of task specificity in which different tasks produce different findings as to whether or not laterality continues as we age.

When finger size was used as a covariate most sex differences disappeared; however, a sex difference still remained when comparing the different pegboards. This suggests that even when using the small pegboard and accounting for finger size, females are still better than males. Our findings do not show the same results as those of Peters et al. (1990) that sex differences disappear after hand size is taking into consideration. The difference between our results and previous literature is discussed in the general discussion. In a related finding, our findings support those of Kilshaw and Annett (1983) as sex differences disappeared once the large pegboard was used.

GENERAL DISCUSSION

Laterality and more specifically asymmetries are studied in different situations and throughout the lifespan (e.g., Gesell and Ames, 1947; Gooderham and Bryden, 2014). Since the pioneering days of Woodworth (1899) different theories have been proposed to understand how manual asymmetries may change with age (e.g., the hemi-aging model, hemispheric asymmetry reduction, and HAROLD model). Each of the models are informative within their own right, however our data best supports a mixture of these models. When the task is a pegboard placing task, children tended to have longer completion times and the times decreased as a function of age (Experiment 1). When the pegboard tasks were used for older adults it seems that they reverted back to child-like performance (Experiment 2) in that the differences in hand performance were demonstrated again. These findings seem to support the hemi-aging model.

The overall view of Grooved Pegboard task in our study seems to suggest that laterality is present at a very early age, then decreases into adulthood, and finally increases again as we age further. However, the limitation of aging research is that most is done using cross-sectional methods which does introduce sampling errors as we cannot definitively say that children who show laterality will grow and still demonstrate laterality once they are over the age of 60. Perhaps biomechanical efficiency (e.g., Bishop et al., 1996; Bryden and Roy, 2006; Bryden et al., 2011; Gooderham and Bryden, 2014) does play a role in determine which hand will be used, and therefore may influence hand performance. Although it may be the case that once we age further, 60+, we may be more confident using our preferred hand and once again forgo biomechanical efficiency and instead use our preferred hand.

One of the strengths of these studies is that the same participants were tested in multiple hand performance tasks to determine if global asymmetries exist for dexterity tasks. This design has allowed us to see that laterality is task specific, in that the Annett pegboard did not show the same finding as the Grooved Pegboard. Rather the HAROLD or the use dependent plasticity models were supported for the Annett Pegboard. Finally the findings of the grip strength demonstrate support for those of Gooderham and Bryden (2014) in stating that hand asymmetries do not change as we become older. Therefore, the question remains, what model is best for understanding the relationship between aging and manual dominance? It seems that asymmetries are task dependent in that different tasks reveal different trends.

By tearing apart the differences in tasks we may begin to understand the different trends associated with aging. The Grooved Pegboard and large pegboard require the participants to grasp a peg that is near them and place the peg into a receptacle that is further away from the participant. Furthermore, the participants are often required to rotate the peg in their fingers in order to successfully place the pegs in the receptacles for the Grooved Pegboard. However, when using the Annett Pegboard the participants grasp the peg starting away from the body and place the peg in a receptacle that is closer to their body. Think about these task differences with reference to the aiming literature. Here it has been revealed that moving the hand away from the body differs from moving it toward the body (Lyons et al., 2006; Heath and Binsted, 2007). The pointing movements toward the body were faster and less variable which supports the findings of Lyons et al. (2006) that aiming toward targets that are closer produces better accuracy. Going back to our results, perhaps differences in asymmetries may exist by changing the location of the receptacles (further or closer to the participant) which may differ in how accurate our movements may be. Therefore, placing a peg that already requires more accuracy (Grooved Pegboard compared to Annett) in a receptacle further from the body may challenge the perceptual-motor system more than placing a peg in a receptacle closer to the body. Our recommendation is that when using different tasks in the future, the different movements that are required to complete the tasks should be considered (see Gooderham and Bryden, 2014) and how directionality or task precision may play a factor.

One other hypothesis that we had was that the size of the fingers would account for sex differences in performance. In previous research (e.g., Peters et al., 1990; Peters and Campagnaro, 1996) finger size was revealed to be an important covariate, however, our data did not fully support this finding. Indeed some of the sex differences did disappear after using finger size as a covariate (Experiment 2), however a few interactions involving sex remained. Specifically females were still better than males when performing the Grooved Pegboard task. Therefore, the differences in performance were not fully accounted by the difference in finger size; rather there are other factors that may account for the sex differences. We must point out, however, that the experimental procedure of Peters et al. (1990) was slightly different than ours. For example, we had individuals perform the tasks with both left and right hands and to incorporate the finger size as a covariate we used a principle component analysis so as to have one covariate measure. This differed from Peters et al. (1990) as only one measure, the right hand, was used for their analyses. Furthermore, when the large pegboard was used, sex differences disappeared which support the findings of Kilshaw and Annett (1983). Therefore, perhaps once individuals' bodies have finished growing the size of the pegs may affect performance differently for males and female. As well perhaps by using the non-dominant arm, the left hand in our experiment, sex differences may be larger and show more of an advantage for females for fine dexterity tasks.

CONCLUSION

It seems that manual asymmetries are a product of aging, as young children explore the world using both hands. It is not until later on that we prefer to use one hand more than the other, and to a point that it may be exclusively used even for contralateral reaching during adolescent years (e.g., Carlier et al., 2006). However, the question whether or not we revert to child-like behavior as we age is not clearly answered. Our results suggest that there were task specific manual asymmetries, as manual dexterity and accuracy requirements may tax the motor systems more in tasks like the Grooved Pegboard and thus reveal preferred hand dominance, while other tasks like the Annett Pegboard do not. Furthermore, the Grooved Pegboard and the use of the non-dominant hand may enhance the differences in sexes, revealing sex differences above that accounted for with finger size; therefore, we a need to standardize methods to get a better sense of lateralization throughout the lifespan. Instead of discussing if asymmetries occur or do not occur, perhaps both occur and we should focus on examining which underlying processes are preserved and which deteriorate with age.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 07 November 2014; accepted: 15 December 2014; published online: 14 January 2015.

*Citation: Sivagnanasunderam M, Gonzalez DA, Bryden PJ, Young G, Forsyth A and Roy EA (2015) Handedness throughout the lifespan: cross-sectional view on sex differences as asymmetries change. Front. Psychol. **5**:1556. doi: 10.3389/fpsyg.2014.01556*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 20 January 2015
doi: 10.3389/fpsyg.2014.01579

Hand preference across the lifespan: effects of end-goal, task nature, and object location

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In the present study we investigate age-related changes in hand preference for grasping and the influence of task demands on such preference. Children (2–11), young-adults (17–28) and older-adults (57–90) were examined in a grasp-to-eat and a grasp-to-construct task. The end-goal of these tasks was different (eat vs. construct) as was the nature of the task (unimanual vs. bimanual). In both tasks, ipsilateral and contralateral grasps were analyzed. Results showed a right-hand preference that did not change with age. Across the three age groups, a more robust right-hand preference was observed for the unimanual, grasp-to-eat task. To disentangle if the nature (unimanual) or the end-goal (grasp-to-eat) was the driver of the robust right-hand preference, a follow up experiment was conducted. Young-adult participants completed a unimanual grasp-to-place task. This was contrasted with the unimanual grasp-to-eat task and the bimanual grasp-to-construct task. Rates of hand preference for the grasp-to-eat task remained the highest when compared to the other two grasping tasks. Together, the results demonstrate that hand preference remains stable from childhood to older adulthood, and they suggest that a left hemisphere specialization exists for grasping, particularly when bringing food to the mouth.

Keywords: grasp-to-eat, visuomotor control, left hemisphere, action intent, development, senescence

INTRODUCTION

Research on human handedness has revealed a preference to use the right hand. These investigations have used a variety of methods, such as the Annett Peg Moving Task (Annett et al., 1979), the Block Building Task (Gonzalez and Goodale, 2009; Stone et al., 2013; Stone and Gonzalez, 2014), the Task Complexity Gradient (Gooderham and Bryden, 2014), and the Tapley–Bryden Dot Marking Task (Tapley and Bryden, 1985), as well as numerous paper-based questionnaires (Oldfield, 1971; Steenhuis and Bryden, 1989; Brown et al., 2006). This right-hand preference for grasping is sensitive to multiple factors, including the nature of the task (i.e., unimanual or bimanual), the end-goal of the task (e.g., grasp to throw, place, or use the object), and the space in which the target object is located [i.e., ipsilateral (on the same side) or contralateral (on the opposite side)] with respect to the grasping hand.

Right-hand use has been shown to be more pronounced for unimanual tasks in which participants are required to pick up one object at a time (Bishop et al., 1996; Corballis, 1997; Calvert and Bishop, 1998; Gabbard et al., 2003; Bryden and Roy, 2006; Carlier et al., 2006; Sacrey et al., 2012) than during tasks in which both hands could potentially be engaged (Gonzalez and Goodale, 2009; Stone et al., 2013; Stone and Gonzalez, 2014). Furthermore, the intent behind an action (i.e., the end-goal of a grasping action; what the individual plans to do with the object after it has been grasped) can also affect hand preference (Geerts et al., 2003; Mamolo et al., 2004, 2006; Bryden and Roy, 2006; Rat-Fischer et al., 2013; Sacrey et al., 2013). For example, Mamolo et al. (2006) found that when right-handed individuals reached for a tool with the intent to use it (compared to just picking it up), right-hand preference increased significantly. In contrast, when individuals were asked to grasp various toys with either the intent to throw it outwards or place it in a nearby box, hand use did not differ between the conditions Bryden and Roy (2006). Similar results have been reported in children. In a recent study, for example, children 1–5 years old were asked to reach for, grasp, and eat cereal (Cheerios® and Froot Loops®), or reach for and grasp blocks in order to manipulate them and build a structure. A right-hand preference was observed in one-year-old children, but only for the grasp-to-eat task. This preference did not surface for the grasp-to-construct task until 4 years of age, at which time it was suggested that it resembled adult behavior (Sacrey et al., 2013).

In addition to the nature and end-goal of a grasp, an object's location in space has also been shown to play an important role in hand selection. For biomechanical reasons, it would make more sense for one to grasp an object with the hand ipsilateral to the object (i.e., right hand for objects in the right space and the left hand for objects in left space). Contrary to this speculation, many researchers have shown that right-hand contralateral grasps in left space are quite common (Leconte and Fagard, 2004; Bryden and Roy, 2006; Mamolo et al., 2006; Gonzalez et al., 2007; Bryden and Huszczynski, 2011; Stone et al., 2013) which refutes the biomechanical speculation. Considering all these factors (task nature, end-goal, and space use), mixed conclusions have been drawn regarding hand preference, and handedness has been thus referred to as a "multifaceted biosocial developmental process" (Michel et al., 2013). Perhaps a way to understand the complexity of hand use/preference is to document its developmental trajectory and examine how the nature and end-goal of the task as well as object location may influence this preference over time.

Given that the vast majority of studies investigating hand dominance have been on developing children or young adults (Annett, 1970; Briggs and Nebes, 1975; Michel, 1981; Fagard and Marks, 2000; Cavill and Bryden, 2003; Bryden and Roy, 2006; Hill and Khanem, 2009; Jacquet et al., 2012; Sacrey et al., 2013; Stone et al., 2013; Scharoun and Bryden, 2014; Stone and Gonzalez, 2014), less is known about changes in hand preference into older adulthood (55+ years) particularly when using objective measures. Most studies, to our knowledge, have used subjective measures (i.e., questionnaires or interviews) to document changes in hand preference in older adults. These studies have reported that with age there is an increase in (the perception of) dominant hand use in right-handers and a decrease in left-handers (Porac et al., 1980; Beukelaar and Kroonenberg, 1986; Hugdahl et al., 1993, 1996; Porac, 1993; Coren, 1995; Porac and Friesen, 2000; Porac and Searleman, 2002, 2006; Hatta et al., 2005; Kumar et al., 2010). The few studies that have objectively tested hand preference in older adults have presented seemingly conflicting results. One reported that the tendency to prefer one hand over the other increases with age (Weller and Latimer-Sayer, 1985), while another concluded that hand-preference lateralization actually decreases as one ages (Kalisch et al., 2006). Furthermore, a recent investigation showed no change in hand preference with age (Gooderham and Bryden, 2014). These studies however, only measured hand preference for unimanual tasks. So, not only are there conflicting results from the few studies that have objectively investigated hand preference across different ages, but we have yet to form a clear picture on whether and how this preference may change as a function of task demands (e.g., nature, end-goal, and space). The main goal of the current investigation was to address this gap in knowledge.

To determine how task nature, end-goal, and object location influence hand preference for grasping across the lifespan, participants aged 2–90 were tested on a unimanual and a bimanual task while hand preference was recorded. For the unimanual task we chose a grasp-to-eat action and for the bimanual task a grasp-to-construct action. Grasp-to-eat was chosen because previous research has shown an earlier emergence of right-hand preference for this action when compared to grasp-to-construct (Sacrey et al., 2013). In the current investigation we used methodology similar to that used in previous reports (Gonzalez et al., 2007; Gonzalez and Goodale, 2009; Sacrey et al., 2013; Stone et al., 2013; Stone and Gonzalez, 2014). For the grasp-to-eat task, participants picked up Froot Loops® unimanually from a tabletop in order to eat them. For the grasp-to-construct task participants were required to pick up building blocks (LEGO®) from a tabletop in order to construct a simple 3D block model. In our previous investigations (see Stone et al., 2013; Stone and Gonzalez, 2014) we have characterized the grasp-to-construct task as *bimanual asymmetric* because the interaction of the two hands is necessary in order to complete it efficiently. Typically one hand is used for grasping the blocks while the other stabilizes the model under construction. Using these two tasks allowed us not only to address the question of whether hand preference changes with age, but also to assess how hand preference is influenced by (1) end-goal (eat vs. construct); (2) task nature (unimanual vs. bimanual); and (3) space use (ipsilateral and contralateral space).

EXPERIMENT ONE

METHODS AND PROCEDURES

Participants

A total of 142 right-handed (by self or parent report) individuals were included in the study and placed into one of three age groups: *Children:* ($n = 80$) ranging from 2 to 11 (50 female), *Young-Adults:* ($n = 37$) ranging from 17 to 28 (25 female), *Older-Adults:* ($n = 25$) ranging from 57 to 90 (16 female) years of age. Children and older adults were recruited from the community of Lethbridge and young-adults from the University of Lethbridge. The study was approved by the University of Lethbridge Human Subjects Research Committee (protocols #2013-040, #2011-022, and #2012-006) and all participants or caregivers gave written informed consent in accordance with the Declaration of Helsinki. Participants were naïve to the purposes of the study.

Apparatus and Stimuli

Handedness questionnaire. A modified version (Stone et al., 2013) of the Edinburgh (Oldfield, 1971) and Waterloo (Brown et al., 2006) handedness questionnaires was given to all participants or caregivers at the end of the experiment. Items in the questionnaire were rated on a scale [+2 (right always) +1 (right usually), 0 (equal), −1 (left usually) and −2 (left always)] depending on how much a hand was preferred for a particular task. Each response was scored as 2, 1, −1, or −2 and a total score was obtained by adding all values. This version included questions on hand preference for up to 22 (ranging from 11 to 22) different tasks. Young and older adults received the questionnaire with 22 items. Children received a questionnaire containing 11 (2–4 years old) or 17 questions (5–11 years old) as not all questions in the questionnarie were appropriate for young children. All scores are expressed as percentage of the highest possible score from the total number of questions answered.

Grasp-to-eat. A total of 20 Froot Loops® were used for the experiment (except for the 2-year-olds who consumed 10 loops). Five of six different colors of loops were placed on the table: purple, pink, orange, yellow, blue, or green. The loops were distributed evenly onto the left and right sides of the table (10 loops per side, 2 of each color; see **Figure 1A** and Supplementary Videos 1, 2). The table was disinfected prior to the task for each participant. The experimenter wore a pair of gloves when placing the loops on the tabletop.

Grasp-to-construct. A total of three models were used for the experiment. Each model contained 5–10 blocks of various colors and shapes. Children aged 2–3 were presented with Mega Bloks® (3.1-6.3 L × 3.1 W × 2.0 cm H) whereas 4 years of age and up were presented with Lego® blocks (ranging in size from < 1.5 L × 0.7 W × 1.0 cm H to 3.1 L × 1.5 W × 1.0 cm H). A previous study in 3- to 5-year-old children showed no difference in hand use between the two different types of blocks (Sacrey et al., 2013). All blocks that made up the models were scattered on a table with a working space of 70 cm deep × 122 cm wide for

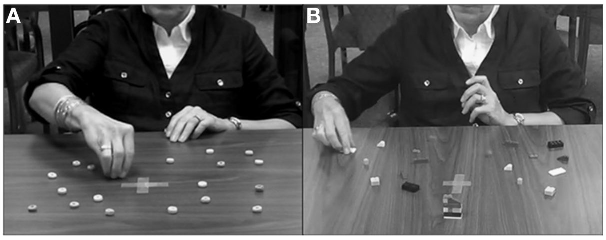

FIGURE 1 | Experimental set up for the (A) Grasp-to-eat and (B) Grasp-to-construct tasks.

the adults, and 60 cm deep × 80 cm wide for the children. The blocks were distributed evenly onto the left and right sides of the table (see **Figure 1B**). No blocks were re-organized between models or replaced after their use (see Supplementary Videos 3–8 for examples of this task).

Procedures

Grasp-to-eat. Participants were seated in front of the table facing the middle of the display. They were then instructed to pick up and eat one loop of a specific color (e.g., a pink loop). Given this instruction participants used only one hand at a time. It was at the participant's discretion to chose with which hand to grasp. This instruction was repeated until no loops remained on the tabletop (see Supplementary Videos 1, 2). No other instruction was given. Therefore, the participant grasped for and consumed 20 loops (i.e., four loops of each color or two loops of each color for the 2-year-olds). The order of colored loops to be grasped was randomized between participants.

Grasp-to-construct. Participants were seated in front of the table facing the middle of the display. A model was placed centrally, approximately arm's length away from the participant. Next, participants were instructed to replicate the model as quickly and accurately as possible from the blocks given on the table. No other instruction was given. Once the model was replicated, both the original and the constructed models were removed from the table and a new model was presented. 2- and 3-year olds who were unable to accurately make a replica of the given model built a model of their choice until all the blocks were used. Used blocks were not replaced after each model was completed. Each participant built three models in total. Model presentation was counterbalanced among participants.

Data Analysis. Both tasks (grasp-to-eat and grasp-to-construct) were recorded on a JVC HD Everio video recorder approximately 160 cm away from the individual with a clear view of the tabletop, target objects (blocks or loops), and participants' hands. All recorded videos were analyzed offline. Each grasp was recorded as a left- or right-hand grasp in the participants' ipsilateral or contralateral space. The total number of grasps was counted to determine a percent for right-hand use (number of right grasps/total number of grasps × 100). Data were analyzed using SPSS Statistics 19.0 for Windows (SPSS Inc., Chicago, IL, USA). Mean and standard errors are reported in percentage for *all* analyses. Bonferroni correction was applied to comparisons where applicable.

RESULTS

No effect of sex was found in any of the analyses, therefore female and male data were combined.

Handedness Questionnaires

A One-Way analysis of variance (ANOVA) with Group (Children, Young-Adults, and Older-Adults) as the independent variable and scores from the handedness questionnaire as the dependent variable was conducted. Results show a main effect of Group [$F_{(2,\ 141)} = 7.54$; $p = 0.001$]. *Post-hoc* analyses revealed that Older-Adults scored higher in the questionnaire (91.6 ± 1.6) than Younger-Adults (71.3 ± 2.3; $p = 0.008$) and Children (77.18 ± 2.8; $p = 0.001$). Scores in the handedness questionnaire did not differ between Children and Younger-Adults ($p = 0.45$).

Grasp-to-eat

Overall right-hand use. Children showed no difficulties in discriminating the loops by color. A One-Way ANOVA with Group (Children, Young-Adults, and Older-Adults) as the independent variable and right-hand use as the dependent variable revealed no significant effect of group [$F_{(2,\ 141)} = 0.3$; $p = 0.72$]. In other words, Children, Young-Adults, and Older-Adults displayed similar rates of right-hand use when picking up the loops to eat (81.3 ± 2.4; 84.1 ± 3.3; 84.3 ± 4.3, respectively).

Contralateral grasps. To assess if hand use changes as a function of space (ipsilateral/contralateral) a repeated measures ANOVA with Group (Children, Young-Adults, and Older-Adults) as the between factor and Hand (Right and Left) used to grasp in contralateral space as the within factor was performed. Results revealed a significant main effect of Hand [$F_{(1,\ 139)} = 250.7$; $p < 0.0001$], no main effect of group [$F_{(2,\ 139)} = 0.1$; $p = 0.8$] and no significant interaction [$F_{(2,\ 139)} = 0.2$; $p = 0.8$]. The right hand was used much more to cross the midline and grasp the loops placed on the left side of the table than the left hand was to grasp the loops on the right side of the table (34.9 ± 1.6 vs. 2.3 ± 0.6). Overall contralateral grasp percentage was similar across all three age groups (Children: 18.3 ± 0.8; Young-Adults: 18.3 ± 1.3; Older-Adults: 19.3 ± 1.6).

Grasp-to-construct

Overall right-hand use. A One-Way ANOVA with Group (Children, Young-Adults, and Older-Adults) as the independent variable and right-hand use as the dependent variable, revealed no significant effect of group [$F_{(2,\ 141)} = 2.1$; $p = 0.11$]. In other words, Children, Young-Adults, and Older-Adults displayed similar rates of right-hand use when picking up the blocks (67.2 ± 1.7; 64.7 ± 1.6; 72.7 ± 3.6, respectively).

Contralateral grasps. A repeated measures ANOVA with Group (Children, Young-Adults, and Older-Adults) as the between factor and Hand (Right and Left) used to grasp in contralateral space as the within factor was performed. Results (see **Figure 2**) revealed a significant main effect of Hand [$F_{(1,\ 139)} = 152.2$; $p < 0.0001$], a main effect of group [$F_{(2,\ 139)} = 5.9$; $p = 0.003$] but

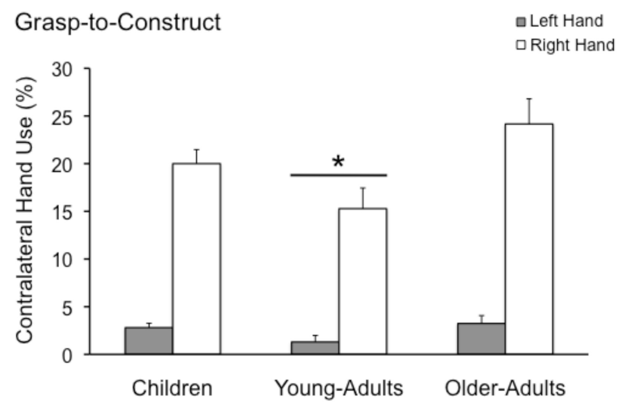

FIGURE 2 | Mean and standard error (in %) for left and right contralateral grasps observed in the grasp-to-construct task by children, young-adults, and older-adults. Note that the young-adults made significantly fewer contralateral grasps when compared to the other two groups. *$p < 0.01$.

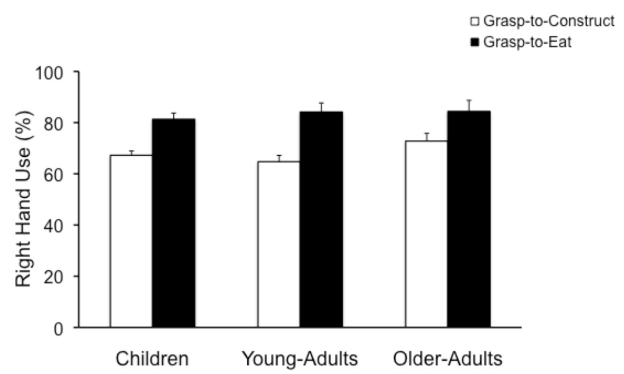

FIGURE 3 | Mean and standard error (in %) for right-hand use in the grasp-to-construct and the grasp-to-eat tasks by children, young-adults, and older-adults. Note the increase in right-hand use for the grasp-to-eat task across the three groups.

no significant interaction [$F_{(2,\ 139)} = 1.6$; $p = 0.2$]. The right hand was used much more to cross the midline and grasp the blocks placed on the left side of the table than the left hand was to grasp the blocks on the right side of the table (19.8 ± 1.2 vs. 2.4 ± 0.3). Pairwise comparisons revealed that the Young-Adult group (8.2 ± 1.0) crossed the midline less often than the Children (11.4 ± 0.7; $p = 0.04$) and the Older-Adult (13.7 ± 1.2; $p = 0.003$) groups. Children and Older-Adults did not differ from each other ($p = 0.33$).

Grasp-to-eat vs. Grasp-to-construct Comparisons

Overall right-hand use. A repeated measures ANOVA with end-goal (grasp-to-eat and grasp-to-construct) as the within factor and Group (Children, Young-Adults, and Older-Adults) as the between factor, revealed a significant main effect of end-goal [$F_{(1,\ 139)} = 47.62$; $p < 0.0001$], no main effect of group [$F_{(2,\ 139)} = 0.88$; $p = 0.41$] and no significant interaction [$F_{(2,\ 139)} = 1.0$; $p = 0.36$]. Right-hand use was greater for the grasp-to-eat task (83.2 ± 2.0) when compared to the grasp-to-construct task (68.2 ± 1.4; see **Figure 3**).

Table 1 | Correlation matrix of all variables.

	Age	Lego	Eat	Handedness questionnaire
Age	1	0.161♦	0.076	0.291**
Grasp-to-construct		1	0.235**	0.048
Grasp-to-eat			1	0.052
Handedness questionnaire				1

♦ *Approaching significance at value of 0.056.*

***Correlation is significant at the 0.01 level (2-tailed).*

Contralateral grasps. A repeated measures ANOVA with end-goal (grasp-to-eat and grasp-to-construct) and hand (Right, Left) used to grasp in contralateral space as the within factors and group (Children, Young-Adults, and Older-Adults) as the between factor was conducted. Similar to the overall right-hand use, there was a main effect of end-goal [$F_{(1,\ 139)} = 77.4$; $p < 0.0001$], no main effect of group [$F_{(2,\ 139)} = 2.5$; $p = 0.08$], and a significant effect of hand [$F_{(1,\ 139)} = 321.2$; $p < 0.0001$]. The only significant interaction was the end-goal by hand [$F_{(1,\ 139)} = 49.9$; $p < 0.0001$] wherein the right hand was used more often to cross the midline in the grasp-to-eat task (18.6 ± 0.7) when compared to the grasp-to-construct task (11.1 ± 0.5).

Correlations

To investigate the possible relationship among age (chronological age 2–90), hand use for the two grasping tasks, and scores on the handedness questionnaire, a correlation (Pearson's r) was conducted on these variables. **Table 1** shows a positive correlation between chronological age and questionnaire scores ($r = 0.29$; $p < 0.0001$). The older the individual, the more they reported to use their right hand on the items in the questionnaire. The correlation between chronological age and right-hand use in the grasp-to-construct task approached significance ($r = 0.16$; $p = 0.056$). The older the age, the more the right hand was used for picking up the blocks. Not surprisingly, the correlation between the two grasping tasks was significant ($r = 0.23$; $p = 0.005$): the more the right hand was used to pick up blocks, the more it was used to grasp loops.

Because hand preference has been shown to change during childhood (Coren et al., 1981; McManus et al., 1988; Gooderham and Bryden, 2014) correlation analyses between age and right-hand use in the grasp-to-construct and grasp-to eat tasks were performed on each age group (children, young-adults, and older-adults). The results showed that correlations between age and right-hand use in the grasp-to-eat and grasp-to-construct tasks approached significance *only* in the children group ($r = 0.211$; $p = 0.06$; $r = 0.219$; $p = 0.051$). There were no significant correlations between age and right-hand use in either grasping task in the young- and older-adult groups (all $p > 0.15$). We followed-up the near significant correlation in children by sub-dividing this group again by age: 2–4, 5–8, and 9–11 years of age. A One-Way ANOVA showed no significant difference between the groups in hand preference for either grasping task [grasp-to-eat: $F_{(2, 79)} = 0.7$; $p = 0.4$; grasp-to-construct: $F_{(2, 79)} = 0.8$; $p = 0.4$]. So although the correlations approached significance, the group analysis was far from significant. We speculate that this is due to the high variability (with standard deviations ranging from 14 to 24%; see **Table 2**) within each sub-group. Importantly and highlighting the main finding of the current study, the between-task differences (grasp-to-eat vs. grasp-to-construct) were significant in all sub-groups of children ($p < 0.01$).

DISCUSSION

The results demonstrated clear differences in right-hand use between the grasp-to-eat and grasp-to-construct actions. Participants in the three age groups displayed greater right-hand preference when picking up the object with intent to eat (loops) vs. picking up the object with intent to construct. This result aligns with a previous report in children that showed increased rates of right-hand use for grasping food vs. blocks (Sacrey et al., 2013). The result from the present study also reinforces the idea that grasp-to-eat actions might be at the origin of population level right-handedness (Flindall and Gonzalez, 2013; Flindall et al., 2014). These investigations of hand kinematics have shown evidence that the grasp-to-eat action executed with the right—but not the left-hand elicits smaller grip apertures during the hand pre-shaping phase of the grasp when compared to other grasping movements. Because smaller grip apertures are typically associated with greater precision, this finding was interpreted as a right-hand advantage for the grasp-to-eat movement. Given this interpretation, it is feasible to speculate that in the current study the greater use of the right hand for the grasp-to-eat task could be related to this kinematic advantage. With respect to our original question however, the results do not resolve if this increase in right-hand use is exclusively due to the end-goal of bringing the object to the mouth. One could argue that the grasp-to-eat task only requires one hand to complete whereas the grasp-to-construct task requires the interaction of both hands. It is therefore possible that the increase in right-hand use is simply due to the unimanual nature of the grasp-to-eat task. To address this possibility, young adult participants were asked to complete the grasp-to-construct task (identical to that in Experiment One) and we contrasted their hand preference to a unimanual version of the same task. For the latter task, the same models were presented to participants, but instead of constructing, they were asked to pick up each block (one at a time) that composed the model and place the block into a container near their body (**Figure 4**). If the unimanual nature of the grasp-to-eat task is what drives the robust right-hand preference, then one would expect similar rates of right-hand use when participants are bringing the block to the container. But, if instead, right-hand use in this unimanual action is lower when compared to the grasp-to-eat task then it would suggest that bringing food to the mouth is lateralized to the right hand.

Table 2 | Percent of total grasps completed with the right hand in each task by children aged 2–11.

Sub-group (age in years)	*N*	Grasp-to-construct (%)	Grasp-to-eat (%)
2–4	21	64.2 ± 3.2	78.0 ± 4.5
5–8	31	66.5 ± 2.9	80.0 ± 4.3
9–11	28	70.2 ± 2.9	81.3 ± 2.4

Values reported are means ± standard errors of each age group. Note that there were no significant differences between sub-groups, but there were significant differences between the two grasping tasks within each sub-group.

EXPERIMENT TWO

METHODS AND PROCEDURES

Participants

Because Experiment One showed no difference in hand preference for grasping among the three age groups (Children, Young-Adults, Older-Adults), only Young-Adults were tested in the second experiment. A total of 37 self-reported right-handed individuals from the University of Lethbridge were included in this study. Participants ranged in age from 17 to 34 (mean age: 20.9 ± 0.5 years). The study was approved by the University of Lethbridge Human Subjects Research Committee (protocol #2011-022) and all participants gave written informed consent in accordance with the Declaration of Helsinki. Participants were naïve to the purposes of the study.

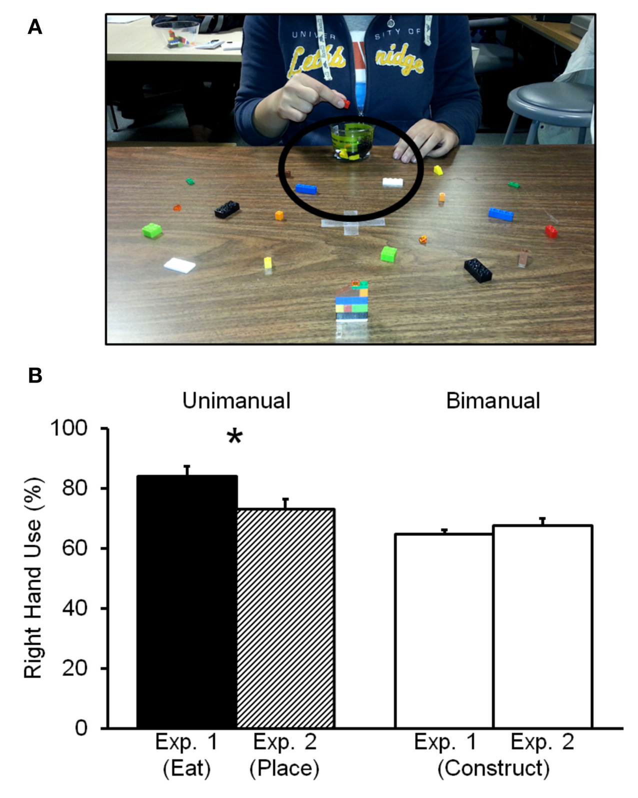

FIGURE 4 | (A) Experimental set up for the Grasp-to-place task (Experiment Two). **(B)** Mean and standard error (in %) for right-hand use in the grasp-to-construct and the grasp-to-eat tasks (Experiment One) and the grasp-to-place task (Experiment Two). $*p = 0.02$.

Apparatus and Stimuli

Handedness questionnaire. The questionnaire was the same as in Experiment One.

Grasp-to-construct. This task was the same as in Experiment One.

Grasp-to-place. This task was set up the same as the grasp-to-construct task, with one modification: a short, clear cup was placed in the front and center of the participant.

Procedures

Grasp-to-construct. Procedures for this task were identical to those in Experiment One.

Grasp-to-place. Participants were seated in front of the table facing the middle of the display. A model was presented centrally, approximately arm's length away from the participant (as in Experiment One). Next, participants were instructed to pick up each block (one at a time) that made up the presented model and place it into the container as quickly as possible. Once all the blocks that made up the model were inside the container, the model was removed and a new model was presented (see Supplementary Video 9). No blocks were replaced after each model was completed. Each participant picked up 30 blocks (10 blocks per model). Model presentation was counterbalanced among participants. As in Experiment One, both tasks were recorded on a JVC HD Everio video recorder approximately 160 cm away from the individual with a clear view of the tabletop, target objects, and participants' hands.

RESULTS

No effect of sex was found in any of the analyses, therefore female and male data were combined.

Handedness questionnaires

The mean score in the questionnaire was 73.3 ± 2.2. To investigate if this group was different from the Young-Adults in Experiment One, a One-Way ANOVA with Experiment (One, Two) as the independent variable and scores from the handedness questionnaire as the dependent variable was conducted. Results show no difference between the two groups [$F_{(1, 73)} = 0.3$; $p = 0.5$].

Grasp-to-construct (bimanual) vs. Grasp-to-place (unimanual) comparisons

A paired samples t-test revealed no significant difference between the two tasks [$t_{(36)} = -1.6$; $p = 0.1$; 67.6 ± 2.5 and 73.0 ± 3.5, respectively]. In other words participants used their right hands to the same extent in both tasks even though one task was strictly unimanual.

Comparison between Experiment One and Experiment Two

To investigate if the finding of greater right-hand use in the grasp-to-eat task (Experiment One) was due to the end-goal of the task (bringing it to the mouth) OR to the intrinsic unimanual nature of the task, we conducted a repeated measures ANOVA. Experiment One and Experiment Two served as the between factors and Task Nature (unimanual, bimanual) as the within factors. This analysis allowed us to investigate if the end-goal of the action influences hand use given that in Experiment One the end-goal was to bring the item to the mouth and in Experiment Two the end-goal was to bring the object to a container. Crucially, in both cases the task was unimanual in nature. A main effect of Task Nature was found [$F_{(1, 72)} = 26.7$; $p < 0.0001$], indicating that participants used the right hand more often during the unimanual task regardless of the Experiment (unimanual: 78.6 ± 2.4; bimanual: 66.1 ± 1.5). There was no main effect of Experiment [$F_{(1, 72)} = 1.4$; $p = 0.2$], but a significant interaction [$F_{(1, 72)} = 8.4$; $p = 0.005$; **Figure 4**]. To investigate this interaction, a series of *post-hoc* analyses (paired-samples- and independent-t-tests) were conducted. First, an independent t-test showed no difference in right-hand use between the bimanual (grasp-to-construct) tasks of Experiment One and Two [$t_{(72)} = -0.9$; $p = 0.3$]. Importantly, the analysis for the unimanual tasks (grasp-to-eat vs. grasp-to-place) between Experiment One and Two *was* significant [$t_{(72)} = 2.2$; $p = 0.02$]. This result suggests that the end-goal and NOT the unimanual nature of these tasks determined the rate at which the right hand was used, namely greater for the grasp-to-eat action. Moreover, and in contrast to Experiment One, paired-samples t-tests revealed that there was no difference between the unimanual (grasp-to-place) and the bimanual task (grasp-to-construct) in Experiment Two [$t_{(36)} = -1.6$; $p = 0.1$]. This result further supports the idea that the grasp-to-eat action might be at the origin of population-level right-handedness.

GENERAL DISCUSSION

To investigate how hand preference for grasping changes as a function of task throughout the lifespan, right-handed participants in three age groups (children, aged 2–11; young adults, aged 18–21; and older adults, aged 57–90) were recorded while performing unimanual self-feeding and bimanual construction tasks. In the unimanual self-feeding task, participants were required to grasp-to-eat Froot Loops®, one at a time, from a pseudo-symmetrical array before them. In the bimanual construction task, participants were required to grasp building blocks from a pseudo-symmetrical array to replicate simple models. Hand preference for these tasks was recorded and analyzed offline to determine the influence of age, task nature (unimanual vs. bimanual), end-goal (build vs. eat), and object location (ipsilateral or contralateral to the grasping hand) on the regulation of hand use. The results showed two interesting findings: first, no difference in hand preference among groups, demonstrating a stable right-hand preference in children, young- and older-adults. Second, right-hand preference was greater for the unimanual grasp-to-eat task when compared to the bimanual grasp-to-construct task. To investigate whether this increased preference was due to the unimanual nature of the task or the end-goal of the action, a secondary experiment was conducted wherein participants performed a unimanual grasp-to-place task to compare to the unimanual grasp-to-eat action. Right-hand preference in the unimanual grasp-to-place task was similar to that of the bimanual grasp-to-build task, both lower than the right-hand preference for the grasp-to-eat task. Finally, analysis of contralateral grasps revealed that participants performed contralateral grasps with their right hands more often than they did with their left hands, although young adults performed significantly fewer contralateral grasps than both children and older adults. Taken together, the results show that hand preference, is significantly affected by the end-goal and spatial demands of the task, but does not change over the course of one's lifespan. Furthermore, they suggest that compared to other seemingly similar movements, the grasp-to-eat action is more lateralized to the right hand.

Few studies have examined changes in hand use across the lifespan. In an early study on age-related changes to manual dexterity, Weller and Latimer-Sayer (1985) found that right-hand motor skills were better preserved than left-hand motor skills in participants of advanced age. When combined with an overall decrease in manual dexterity, this study suggests that the gap between right- and left-hand performance increases as one ages. In contrast, a more recent study by Kalisch et al. (2006) found that dominant-hand speed and precision advantages observed in young adults are lost later in life, and that this change is accompanied by a shift in hand-preference for commonplace tasks. In other words, that study found that as right-hand advantage declines, so does right-hand preference in favor of a more ambidextrous approach to everyday activities. A third study, by Gooderham and Bryden (2014) used a multifaceted approach to measuring hand dominance in a large cross-sectional study and found that, once firmly established in adulthood, the level and degree of hand-dominance does not change with increasing age. The results of the current study support that finding, as hand-preference for the grasp-to-eat, grasp-to-construct, and grasp-to-place tasks showed no age-related changes between any of our groups. In contrast with Gooderham and Bryden (2014), however, we observed no difference in laterality between children and other age groups in the behavioral task. This may be due in part to the differences in ages between children in both studies; Gooderham and Bryden tested children aged 2–4, whereas the age of our sample of children ranged from 2 to 11 years old. The 11-year-old children would have been considered young adolescents by Gooderham and Bryden. More likely, the difference in results may stem from methodological differences between the studies. Gooderham and Bryden inferred hand-dominance through motor-skill performance and a complexity-related switch point, whereas we asked participants to perform simple everyday activities and inferred lateralization of dominance from direct observation of hand preference. With regards to the handedness questionnaire, the significant correlation between age and handedness scores suggest that the older the individual the more right-handed they perceive themselves to be. This is in agreement with a previous report which concluded that elderly subjects rate themselves as strongly right-handed regardless of their objective hand use (Kalisch et al., 2006). The primary finding of our study is consistent with these results, in that lateralization of hand dominance neither increases nor decreases as one ages beyond adulthood, regardless of one's subjective perception.

The second finding of the current study was that the end-goal of an action plays a significant role in determining whether or not one will use their right hand to perform that action. In the unimanual self-feeding task, participants of all ages used their right hands significantly more often than they did during the bimanual construction or unimanual placement tasks. This increased right-hand preference also extended to contralateral grasps, which were significantly more common when the objective of the grasp was to eat, rather than place or manipulate the target. As the mechanical requirements of the different types of grasp are ostensibly identical, the decision to more often use the right-hand for grasp-to-eat tasks suggests a fundamental difference between the neurological origins of the grasps. This presumption is supported by findings from Sacrey et al. (2013), who found that children develop a right-hand preference for grasp-to-eat tasks several years earlier than they do for grasp-to-build tasks. Furthermore, Flindall and Gonzalez (Flindall and Gonzalez, 2013, 2014, submitted; Flindall et al., 2014) have found a left-hemisphere/right-hand advantage in the kinematics of grasp-to-eat/hand-to-mouth actions that is absent from grasp-to-place actions. Specifically, when grasping a small food item with intent to eat, participants produce tighter maximum grip apertures during the outgoing movement than when grasping the same item to place it in a receptacle near the mouth. This task difference in hand pre-shaping is predominantly lateralized to the right hand, regardless of a person's overall hand preference (Flindall and Gonzalez, 2013; Flindall et al., 2014). Taken together, these findings all support a theory of human motor cortex organized around a catalog of movements based on end-goal, rather than mechanical requirements (Graziano et al., 2002, 2004, 2005; Fogassi et al., 2005; Graziano, 2006, 2009; Bonini et al., 2011, 2012; Flindall and Gonzalez, 2013, 2014). The results from the present study demonstrating greater right-hand use for the grasp-to-eat task further support the proposal that this type of action might be at the forefront of population level right-handedness in humans.

In conclusion, the current study investigated lateralization of motor dominance as it relates to task nature, end-goal, and space constraints by observing hand preference in simple grasp-to-eat, grasp-to-construct, and grasp-to-place tasks. To assess whether and how hand preference changes throughout the lifespan, these tasks were performed by children, young adults, and seniors. A right-hand preference for all tasks was observed, however, this preference was greater during the grasp-to-eat task. This effect was consistent throughout all age groups. These results further our knowledge of the developmental trajectory of manual asymmetries across the lifespan.

ACKNOWLEDGMENTS

This project was funded by a grant from the National Science and Engineering Research Council (NSERC Canada) to Claudia L. R. Gonzalez and postgraduate NSERC to Kayla D. Stone.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2014.01579/abstract

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 08 October 2014; accepted: 20 December 2014; published online: 20 January 2015.

Citation: Gonzalez CLR, Flindall JW and Stone KD (2015) Hand preference across the lifespan: effects of end-goal, task nature, and object location. Front. Psychol. ***5****:1579. doi: 10.3389/fpsyg.2014.01579*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in PSYCHOLOGY

ORIGINAL RESEARCH ARTICLE
published: 03 February 2015
doi: 10.3389/fpsyg.2015.00058

Left-handers look before they leap: handedness influences reactivity to novel Tower of Hanoi tasks

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A sample of 203 task naïve left- and right-handed participants were asked to complete a combination of the 3- and 4-disk Towers of Hanoi (ToH), manipulating novelty and complexity. Self-reported state anxiety and latency to respond (initiation time) were recorded before each ToH. Novelty had a major effect on initiation time, particularly for left-handers. Left-handers had a longer latency to start and this was significantly longer on the first trial. Irrespective of hand-preference, initiation time reduced on the second trial, however, this was greatest for left-handers. Condition of task did not systematically influence initiation time for right handers, but did for left-handers. State anxiety was influenced by task novelty and complexity in a more complicated way. During the first trial, there was a significant handedness × number of disks interaction with left-handers having significantly higher state anxiety levels before the 3-disk ToH. This suggests that the initial reaction to this task for left-handers was not simply due to perceived difficulty. On their second trial, participants completing a novel ToH had higher state anxiety scores than those completing a repeated version. Overall, left-handers had a larger reduction in their state anxiety across trials. Relating to this, the expected strong positive correlation between state and trait anxiety was absent for left-handed females in their first tower presentation, but appeared on their second. This was driven by low trait anxiety individuals showing a higher state anxiety response in the first (novel) trial, supporting the idea that left-handed females respond to novelty in a way that is not directly a consequence of their trait anxiety. A possible explanation may be stereotype threat influencing the behavior of left-handed females.

Keywords: handedness, Tower of Hanoi, task complexity, novelty, state anxiety, trait anxiety

INTRODUCTION

Research conducted from the 1970's through to the early 1990's examining the relationship between handedness and anxiety has produced a number of inconsistent and inconclusive findings. A common finding is that left-handers are more anxious, and worry more, than their right-handed counterparts (e.g., Orme, 1970; Hicks and Pellegrini, 1978; Davidson and Schaffer, 1983; Dillon, 1989). More specifically Orme (1970) found that left-handers reported themselves to be more introvert and shy than right-handers, Hicks and Pellegrini (1978) reported that left- and mixed-handers were significantly more anxious and Davidson and Schaffer (1983) reported higher trait anxiety levels in left-handers. Additional research around this time focussed upon the relationship between consistency of handedness (consistent versus inconsistent handedness) and anxiety. Wienrich et al. (1982) reported that consistent handers (irrespective of a left or right preference) had higher levels of anxiety than inconsistent handers, and Merckelbach et al. (1989) reported that consistent right-handers demonstrated higher social anxiety than left-handers. On the other hand, Mueller et al. (1991) examined differences in test anxiety between left- and right-handers and found that high-test anxiety did not affect left-handers any more than it affected right-handers. Other research has found no relationship between handedness and anxiety (e.g., French and Richards, 1990; Beaton and Moseley, 1991).

However, there has been a recent resurgence in research examining the relationship between handedness and anxiety. These studies have attempted to address some questions left unanswered by previous research. One key aspect of this recent research has been the use of the State Trait Anxiety Inventory (STAI; Spielberger et al., 1983) as the chosen measure. The STAI is arguably a good measure as it has a solid history of use in both clinical (e.g., Karch et al., 2008) and general psychological research (e.g., Baeken et al., 2011), and has good reliability (Bieling et al., 1998; Vautier and Pohl, 2009). The STAI has been designed to capture two main aspects of anxiety. State anxiety is a response to a given situation, and exists as an emotional response elicited by the situation, and expressed as a transient state of subjective worry, apprehension and general nervousness (Gerstorf et al., 2009; Roup and Chiasson, 2010). Tovilović et al. (2009) describe Trait Anxiety as a stable individual tendency to respond anxiously to all situations, and argue that this is really a measure of the likelihood that the individual will express state anxiety in a given situation. Although these two measures are conceptually linked, they are only moderately positively correlated (average correlation of 0.65, according to Spielberger et al., 1983). State anxiety is arguably the most appropriate measure to focus on, as it is more closely related to immediate behavioral responsiveness (Tovilović et al., 2009). Wright and Hardie (2012) examined state and trait anxiety differences between left- and right-handers. In contrast to previous studies (e.g., French and Richards, 1990) state anxiety was measured within the context of an experimental situation (i.e., introducing a mildly stressful scenario, allowing participants to have something to react to). Wright and Hardie (2012) found that left-handers reported higher levels of state anxiety but there was no difference in trait anxiety. They also demonstrated that when Trait Anxiety was controlled for, left-handers still showed a higher level of state anxiety compared to right-handers. This supports the notion that state anxiety differences are the most appropriate measurement to record when examining the reaction to a particular situation. Lyle et al. (2013) investigated the relationship between state anxiety, trait anxiety, worry and consistency of handedness. They found that inconsistent right-handers had lower levels of state and trait anxiety than consistent right-handers. In left-handers there was no relationship between consistency of handedness and anxiety, but inconsistent left-handers had higher levels of anxiety than inconsistent right-handers. While the rationale behind this difference remains unclear, Lyle et al. (2013) suggest that left-handers and right-handers may differ in terms of what triggers anxiety, and that this could "differ based on subjective differences in environmental experiences" (p. 14).

Studies carried out with non-human primates and human infants offer additional support to the relationship between handedness and anxiety. Westergaard et al. (2000) reported that high cortisol levels at 6 months in rhesus macaques were predictive of a left-hand bias at both 6 and 12 months of age. Adding to this, Westergaard et al. (2001) found an association between a left-hand preference and higher levels of the stress hormone cortisol in infant rhesus monkeys. Based on these findings Westergaard et al. (2001) argue that greater stress during infancy can *cause* a left-handed preference in rhesus monkeys. However, an alternative explanation of this finding might be that left-handedness, and thus right hemisphere motor dominance, increases anxiety and stress rather than stress causing the hand preference.

Very little research exists examining the relationship between hand preference and novelty. Of these studies, many involve non-human participants, and several report that if a task is new or unnatural to a left-hander this will increase their anxiety levels. For example, Cameron and Rogers (1999) found that there was a difference between left- and right-handed marmosets in their response behavior toward a novel object. They found that left-handers took significantly longer to approach and touch the novel object. Rogers (1999) replicated this finding and reported a difference in approach behavior to a novel object between left-handed and right-handed marmosets. Gordon and Rogers (2010) also found that right-handed marmosets were quicker to approach and interact with novel stimuli while Braccini and Caine (2009) found that left-handed marmosets took longer to approach and interact with novel food. These findings extend earlier work by Hopkins and Bennett (1994) who reported that left-handed chimpanzees were slower to approach novel objects than right-handed chimpanzees. However, Watson and Ward (1996) investigated temperament and problem-solving in the small-eared bush baby and found that left-handed bush babies were *less* inhibited in their approach to novel objects than right-handed subjects.

Thus, it appears that the introduction of a novel object may differentially influence the approach behavior of left-handers and right-handers. Rogers (1999) suggested that these findings could be explained by the differences in hemispheric specialization for processing novel stimuli and controlling emotional responses. She proposed that the left hemisphere controls exploratory behavior while the right hemisphere is associated with inhibitory or avoidance behavior. This would suggest that right-handers would be influenced by the dominant left hemisphere and would be more likely to demonstrate exploratory behavior, while left-handers would be more likely to be controlled by the right hemisphere and demonstrate inhibitory behavior. Supporting this notion is work by Davidson and colleagues (e.g., Davidson, 1985, 1992, 1995, 1998) linking behavioral avoidance and behavioral inhibition to the right-hemisphere. Sutton and Davidson (1997) also argue that the left-hemisphere is implicated in approach behavior. This suggests a model of hemispheric specialization in terms of interacting with the world that links the right-hemisphere to avoidance and the left-hemisphere to approach (see Rutherford and Lindell, 2011 for a review). In terms of evidence for the right-hemisphere, Shackman et al. (2009) found that individuals that are high in self-reported behavioral inhibition show an increased right dorsolateral prefrontal cortex resting activity, compared to low inhibited individuals. This lateralised pattern is further supported by studies linking the right-hemisphere to infants' temperamental shyness, anxiety, and behavioral inhibition (Schmidt et al., 1999; Fox et al., 2001). Assuming that measures of lateral preference are also indicators of hemispheric dominance (Kinsbourne, 1997; Jackson, 2008) then a lateral preference is indicative of a preference for the contralateral hemisphere. For example, left-handers have been shown to self-report themselves as more behaviorally inhibited than right-handers (Wright et al., 2009). Arguably, this relationship between left-handedness and behavioral inhibition has become relatively well established, covering comparative evidence (Cameron and Rogers, 1999; Rogers, 2009), studies using self-reports (Hardie and Wright, 2013, 2014; Lyle et al., 2013) and through a series of behavioral studies (Wright et al., 2004, 2013; Wright and Hardie, 2011).

Although this work supports the proposal that the right hemisphere is associated with fear and avoidance behavior and is linked to the inhibitory system, Goldberg et al. (1994) have suggested an alternative explanation. They argue that the right hemisphere is specialized for novelty and that this hemisphere is more spontaneous, unreflective and does not effectively organize information but instead uses a type of trial and error system. Goldberg et al. (1994) suggest that the left hemisphere is concerned with a preference for familiarity and is more reflective and organized when processing information. Goldberg's (2001) work does not systematically evaluate possible hemispheric differences related to hand preference. However, Goldberg (2001) himself suggests that left-handers appear to be more responsive to novelty than right-handers, and have a more varied distribution of cognitive processing, including a reversal in this set-up.

Although there is little actual evidence to support this, it is possible that such differences in processes may contribute to differences when confronted with novelty. Work by Piper et al. (2011) provides evidence that left-handers may process novel situations differently from right-handers. During the novel image detection phase of the '*novel-image novel-location*' spatial learning paradigm, left-handers were significantly more sensitive to changes, correctly noticing more insertions and details relating to the change.

Another factor that has to be taken in to account when considering anxiety levels and problem-solving is task complexity. A straightforward interpretation would argue that it is more likely that higher levels of anxiety will be produced when a task is more complex (Hembree, 1988). Contrary to this, Druckman and Swets (1988) stated that simple tasks actually require a high state of arousal by participants in order for them to remain focussed on the task. They add that as task complexity increases the level of arousal should decrease. Fink and Neubauer (2004) suggest a relationship between task complexity and stress in introvert/extravert participants. They reported that the easier a task was, the more likely introverted participants were to display lower cortical activation (suggesting that they were not as stressed). However, in more complex test conditions introverts showed higher cortical activation than extraverts.

In order to understand relationships between handedness and approaches to problem-solving we have investigated behavioral differences between left- and right-handers in novel tasks (Wright et al., 2004, 2013; Wright and Hardie, 2011). For example, Wright et al. (2004) found that left-handers took significantly longer to begin the 3-disk Tower of Hanoi (ToH) task. We proposed that one explanation for differences in approach behavior between left- and right-handers could be that left-handers might be experiencing higher levels of state anxiety in novel situations (Wright and Hardie, 2012).

The ToH, is cited as a commonly used test of executive function (e.g., Anderson and Douglass, 2001; Lezak et al., 2004), and executive functioning itself is a term used to describe a collective set of higher order cognitive functions (Beratis et al., 2013). These are thought to include inhibition, planning, working memory and cognitive flexibility (Goldstein et al., 2014). Work examining performance on the ToH, has strongly linked it to inhibition (Miyake et al., 2000), as overall success depends upon inhibiting moves that may appear to be correct but are wrong. Many studies use the ToH in the context of learning and memory, but few studies have systematically compared the 3- and 4-disk versions of the task. Mataix-Cols (2003) used a single presentation of the 3-disk version, but multiple presentations of the 4-disk task, and found that subclinical obsessive-compulsive (OC) individuals were poorer at solving the 3-disk version, although few differences were found in the 4-disk performance. Many studies make use of repeated trials of the ToH, and rarely report first move data when used in a novel situation. Contrary to this, Bustini et al. (1999) reported mean 'planning time' (i.e., time to make first move) for multiple trials of both 3- and 4-disk versions, comparing schizophrenic patients to matched controls. In this study, the patients had a longer mean planning time in both versions, but it was not significantly longer and only controls had a shorter time for the 3-disk version. Importantly, only right-handers were tested in this study. Guevara et al. (2013) examined developmental effects, again with only right-handed participants aged between 11 and 30 years old. They modified the 3-disk ToH with an additional rule – participants can move the disk to an adjacent peg only (i.e., no peg can be skipped over), increasing the solution to 26 moves. It was shown that time to make the first move averaged around 2–3 s, with no between group differences. Therefore the relationship between tower version and 'time to make the first move' is not straightforward. In the current study we will investigate these concepts further by manipulating both the novelty and complexity levels of the Tower of Hanoi Task, while adding the additional factor of handedness. Each participant will be asked to complete the Tower of Hanoi twice and will be in one of four conditions.

CONDITION 1

Participants complete the 3-disk task, followed by a second 3-disk task (3–3) – novel verses non-novel version of the task and the simplest version of the task so complexity does not change.

CONDITION 2

Participants complete the 3-disk task, followed by the 4-disk task (3–4) – simple and novel version of the task is completed first then the complexity increases in the second task and the task is slightly different due to the number of disks changing but the rules are the same.

CONDITION 3

Participants complete the 4-disk task, followed by a second 4-disk task (4–4) – novel verses non-novel version of the task but a more complex version of the task (so again complexity does not change).

CONDITION 4

Participants complete the 4-disk task, followed by the 3 disk task (4–3) – more complex but novel version of the task is completed first then the complexity decreases in the second task and the task is slightly different due to the number of disks changing but the rules are the same.

State anxiety and trait anxiety levels will be measured along with degree and direction of hand preference. On each Tower of Hanoi task time taken to move the first disk, number of moves taken and task completion time will be recorded. It is hypothesized that

HYPOTHESES

Novelty

1 State anxiety levels will be higher and initiation time will be longer in left-handers when they complete the Tower of Hanoi for the first time only.

Complexity

2a. State anxiety levels will be higher and initiation time will be longer in left-handers when they complete the more complex 4-disk Tower of Hanoi.

2b. If complexity is important, when this increases on the second trial (i.e., 3–4) the state anxiety levels and initiation times should increase, compared to when this decreases on the second trial (i.e., 4–3).

MATERIALS AND METHOD

PARTICIPANTS

Two hundred and three participants took part in the study, all were university staff and students. Eighty-six participants were left-handed (39 males and 47 females) and 117 were right-handed (54 males and 63 females). The modal age category was 18–29 years. The Tower of Hanoi (ToH) task was completed twice by each participant where levels of novelty and complexity were manipulated (3–3; 3–4; 4–4; 4–3 disks). Participants were randomly assigned within their sex and handedness groups into conditions. All participants gave their informed consent to participate in the study. The study was approved by the School of Social and Health Sciences Ethics Committee and abided by the ethical regulations of the British Psychological Society.

MATERIALS AND APPARATUS

State Trait Anxiety Inventory (Spielberger et al., 1983)

The state anxiety questionnaire consisted of 20 short statements. The directions on the questionnaire required participants to answer according to how they felt *right at that moment*. State anxiety statements included 'I am tense' and 'I feel calm' and these were answered on a four-point Likert scale ranging from '1 = not at all' to '4 = very much so.' Ten of the 20 statements were reverse scored and total scores ranged between 20 and 80. The trait anxiety scale consisted of another 20 statements which were also answered on a four-point Likert scale ranging from '1 = almost never' to '4 = almost always.' Directions instructed participants to read each statement and answer in relation to how they *generally feel*. Statements this time included 'I lack self-confidence' and 'I am calm, cool and collected.' Responses were totalled and scores ranged from 20 to 80. A score of 20 on both scales indicated low anxiety levels and 80 indicated high anxiety levels.

Tower of Hanoi

The Tower of Hanoi Task consisted of three pegs and up to four colored disks stacked on one of the pegs. Counterbalancing was carried out so that half of all left-handed and right-handed participants began the task with the disks stacked on the left peg and worked to move all of the disks to the last empty peg on the right. The other half of the left- and right-handers began with the disks stacked on the peg on the right side and aimed to stack them all on the empty peg on the left. The disks were stacked on the peg in order of size with the largest one on the bottom and the smallest one on the top. The two empty pegs were used to move the rings from the full peg to the last empty peg. A cardboard cover was used to conceal the Tower of Hanoi to ensure that participants could not see it. A stopwatch with a split-time function was used which allowed the initial first move time to be stored alongside the total completion time. To ensure consistency the same researcher measured the initiation and completion times on the Tower of Hanoi. The process of measuring and recording the ToH variables was identical to Wright et al. (2004). Written instructions were given to participants outlining the rules of the task and depicting the initial state and goal state. Participants were instructed that they were going to see three pegs and on one of the pegs there would be a number of disks (either three or four depending upon the condition) stacked on it (there were separate instructions for the 3-disk and the 4-disk trials). The rules were that only 1-disk could be moved at a time, a larger disk could not be placed on a smaller disk and the participant should only use their dominant hand to carry out the task. A different set of instructions were given to participants when they did the Tower of Hanoi for the second time. The instructions again outlined the rules of the task and showed the initial state and goal state but either stated that the participant was going to be asked to do **exactly** the same task again (if they were in the 3-disk, followed by 3-disk; or 4-disk, followed by 4-disk condition) or that they would be asked to do a ***similar*** task but that a disk would be added (if they were in the 3-disk, followed by 4-disk condition) or taken away (if they were in the 4-disk, followed by 3-disk condition). The optimal solution for the 3-disk ToH was seven moves and for the 4-disk ToH, 15 moves.

Handedness questionnaire

Following Peters's (1998), Wright et al. (2004) handedness questionnaire was used to measure participant's handedness. The original version is a 25-item scale scored using a five point Likert scale (left-hand always, left-hand mostly, either hand, right-hand mostly and right-hand always). The five points on the scale are assigned values from -2 (always use the left hand) through to 2 (always use the right hand) and each item is scored individually then totalled to give an overall handedness score. A total positive value indicates a right-hand preference and a total negative value indicates a left-hand preference.

PROCEDURE

Participants were asked to complete Peters (1998) handedness questionnaire. Participants were then given a copy of the instructions for the novel problem-solving task (either the 3-disk or 4-disk Tower of Hanoi). After reading the Tower of Hanoi instructions participants were asked to complete the state anxiety questionnaire of the STAI to measure current levels of anxiety. They were instructed to answer the questions according to how they felt *right at that time*. Once this was completed participants were instructed to solve the Tower of Hanoi (3- or 4-disk depending on the condition that they were assigned to) with their preferred hand. The Tower of Hanoi was concealed with a large cardboard cover and this was removed when the participant was ready to begin the task. When the participant made *physical contact* with the first disk the experimenter recorded the initiation time on the split-time stopwatch. The experimenter also kept a note of the number of moves the participant took to solve the Tower of Hanoi. When the participant had successfully solved the Tower of Hanoi the stopwatch was stopped and the total time taken to complete the task was recorded. In order to create a delay between the two tasks and purely to act as a distractor, participants had their digit ratio measured on both hands. This created a gap of ~5 min. A second set of Tower of Hanoi instructions was then given to participants. These instructions differed depending on the condition that each participant was assigned to. Participants who were in the condition where they did the 3-disk or 4-disk Tower of Hanoi twice (3–3; 4–4) were given an identical set of instructions to the ones they received the first time except this time it was emphasized that the task was **exactly** the same as they did the first time and that the rules were the same as the first trial. Those who completed the 3-disk Tower of Hanoi or 4-disk Tower of Hanoi first were given a set of 4-disk and 3-disk Tower of Hanoi instructions respectively (3–4; 4–3) which again outlined the rules and showed a picture of the initial and goal states. When participants had read the instructions they were asked to fill in a second state anxiety questionnaire and then complete the second trial of the Tower of Hanoi. The side of the initial disk stack was counterbalanced across all participants so, for example, half of the left-handed males started from the right when doing the 3-disk Tower of Hanoi and the other half started on the left hand side. This was the same for the other sex and handedness groups across the 3-and 4-disk trials. Again initiation time, number of moves and completion time were recorded. Only participants who had never solved the Tower of Hanoi before were included in the sample to ensure that the task remained novel to all participants throughout the experiment. Finally, the trait anxiety questionnaire was completed and participants were fully debriefed.

RESULTS

Table 1 summarizes the results for both tower presentations, listed separately for left- and right-handers. For the first tower, all participants were naïve and so the tower was novel, but there were two conditions differing in complexity (3-disk versus 4-disk). For the second tower, there was the added complication of whether the task was the same (3–3, 4–4), made easier (4–3) or more difficult (3–4).

STATE ANXIETY

State anxiety on first tower (novel task)

We initially examined the difference between left- and right-hander's state anxiety levels (state anxiety before completing the ToH for the first time) irrespective of the number of disks the participant completed in the trial, in order to look for a *general* effect of the task on anxiety. There was no significant difference between state anxiety scores of left- ($m = 36.7$) and right-handers ($m = 35.1$) before their first Tower of Hanoi task $t(201) = 1.29$, $p = 0.199$. **Table 1** indicates that left-handers had higher state anxiety levels than right-handers when completing the three-disk ToH in the first task but right-handers have slightly higher state anxiety scores before completing the four disk ToH in the first task.

A 2 (gender) × 2 (hand preference) × 2 (number of disks) between subjects ANOVA was carried out to investigate individual state anxiety scores before their first ToH task. There was no significant main effect of gender $F(1,195) = 1.8$, $p = 0.18$, hand preference $F(1,195) = 1.46$, $p = 0.23$, or number of disks $F(1,195) = 3.27$, $p = 0.07$. However, there was a significant interaction between handedness and number of disks $F(1,195) = 5.0$, $p = 0.026$, partial $\eta^2 = 0.03$, observed power = 0.6. **Figure 1** shows that left-handers were most anxious prior to starting the 3-disk Tower of Hanoi. *Post hoc* pairwise comparisons (Tukey) showed that the only significant difference was between the left-handers ($p = 0.05$) where participants had a higher state-anxiety score when preparing to start the 3-disk tower.

Table 1 | Summary of results.

			Trait anxiety	State anxiety	Initiation time	Moves	Time
Tower 1							
	3-Disk	**Total**	**40.1 (9.0)**	**36.7 (8.7)**	**4.4 (4.8)**	**11.9 (6.2)**	**50.6 (37.4)**
		Left	41.8 (8.4)	39.4 (8.3)	5.8 (5.9)	11.4 (86.9)	45.6 (33.2)
		Right	38.9 (9.3)	34.9 (8.5)	3.4 (3.6)	12.2 (5.7)	54 (40)
	4-Disk	**Total**	**40.9 (10.6)**	**34.8 (10)**	**4.0 (3.9)**	**26.9 (10.2)**	**116.6 (73.2)**
		Left	39.5 (9.4)	34.2 (9.7)	4.5 (4.4)	26.7 (9.8)	110.5 (65.1)
		Right	42 (11.4)	35.3 (10.3)	3.6 (3.4)	27.1 (10.7)	121.4 (79.3)
Tower 2							
	3–3	**Total**	**39.8 (9.6)**	**29.3 (7.6)**	**1.3 (.5)**	**10.1 (4.4)**	**33.5 (20.6)**
		Left	41.8 (8.6)	30.6 (7.1)	1.5 (.7)	9.3 (2.3)	31.7 (19.5)
		Right	39.0 (10)	28.8 (7.8)	1.2 (.4)	10.5 (5)	34.2 (21.2)
	3–4	**Total**	**39.7 (8.8)**	**34.3 (7.5)**	**2.5 (2.4)**	**27.4 (13.4)**	**100.7 (93.4)**
		Left	41.9 (8.4)	35.4 (5.9)	3.0 (2.9)	25.3 (12.1)	93.6 (82.5)
		Right	37.4 (8.7)	33 (8.9)	1.9 (1.6)	29.6 (14.5)	108.3 (105)
	4–4	**Total**	**39.0 (9.1)**	**30.5 (8.5)**	**2.1 (1.2)**	**25.5(11.6)**	**63.5 (44.2)**
		Left	37.6 (8.2)	29.7 (7.9)	2.2 (1.4)	25.6 (11.6)	62 (45.3)
		Right	40.4 (10)	31.4 (9.2)	2.0 (1.1)	25.3 (11.8)	65.2 (43.8)
	4–3	**Total**	**44.0 (11.4)**	**34.7 (10.9)**	**1.4 (0.9)**	**12.3 (9.3)**	**39.1 (30.2)**
		Left	42.9 (10.8)	34.1 (12.8)	1.7 (1.4)	11.3 (3.7)	34.8 (18.8)
		Right	44.5 (11.8)	35.1 (10)	1.2 (0.5)	12.8 (11.3)	41.4 (34.9)

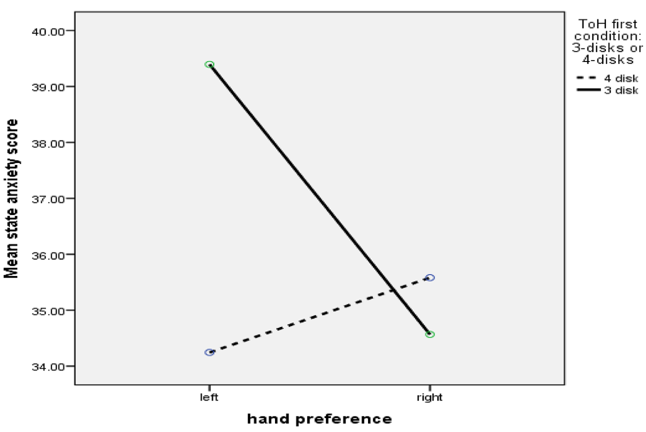

FIGURE 1 | Hand preference by disk number interaction (state anxiety scores).

State anxiety on second tower (novelty and complexity)

In order to investigate the hypotheses, response to the second tower can be examined in two main ways; the response to the second tower can be examined itself, followed by a comparison between the first and second trials. A 2 (hand preference) × 2 (number of disks) × 2 (Novelty) between subjects ANOVA was initially carried out to investigate state anxiety scores before the second ToH task. There was no significant main effect of hand preference $F(1,195) = 0.09$, $p = 0.76$, or number of disks $F(1,195) = 0.23$, $p = 0.64$. There was a significant main effect of novelty $F(1,195) = 11.48$, $p = 0.001$, partial $\eta^2 = 0.06$, observed power = 0.9, where individuals encountering novel versions of the tower had significantly more state anxiety. There were no significant interactions.

STATE ANXIETY DIFFERENCES (INFLUENCE OF CONDITION)

A 2 (hand preference) × 4 (condition) between subjects ANOVA was then used to investigate the mean difference in state anxiety between the first and second trials. There was a significant main effect of hand preference $F(1,195) = 4.9$, $p = 0.028$, partial $\eta^2 = 0.03$, observed power = 0.6, with left-handers showing a significantly larger drop in their state anxiety when encountering the task for the second time. There was a significant main effect of disk-condition $F(3,195) = 7.6$, $p < 0.001$, partial $\eta^2 = 0.1$, observed power = 1. Tukey *post hoc* tests were carried out to further investigate the significant state anxiety difference scores between the four disk-conditions. **Table 2** indicates that the largest reduction was for the 3–3 condition (easy task completed twice), there were significant state anxiety score differences between the **3–3** and 4–4 ($p < 0.001$) and between the **3–3** and 3–4 ($p = 0.006$) conditions. No other comparisons were significant.

INITIATION TIME

Initiation time on first tower (novel task)

There was a significant difference between initiation times scores of left- ($m = 5.1$ s) and right-handers ($m = 3.5$ s) before their first Tower of Hanoi task $t(201) = 2.7$, $p = 0.007$, with left-handers taking significantly longer. **Table 1** includes figures broken down by disk number. Left-handers took longer to move the first disk in general and the longest initiation time was taken by left-handers in the 3-disk condition.

A 2 (gender) × 2 (hand preference) × 2 (number of disks) between subjects ANOVA was carried out to investigate the time taken to move the first disk of the first ToH task (initiation time). There was a significant main effect of gender, $F(1,195) = 11.4$, $p = 0.001$, partial $\eta^2 = 0.1$, observed power = 0.9 There was a significant main effect of hand preference $F(1,195) = 6.7$, $p = 0.010$, partial $\eta^2 = 0.03$, observed power = 0.7 (with left-handers taking

Table 2 | Mean state anxiety and initiation time difference scores (Time 1 – Time 2) between the first and second Towers of Hanoi (novel vs. not novel) when disk number is considered.

Hand-preference	Condition	Mean state difference*	Total	Mean initiation difference*	Total
Left	3–3	8.6 (8.9)		6.2 (8.1)	
Right	3–3	6.0 (5.7)		2.3 (3.7)	
	3–3 Total		**6.8 (6.8)**		**3.4 (5.6)**
Left	4–3	6.3 (10.2)		1.9 (3.3)	
Right	4–3	2.7 (7.3)		1.4 (3.6)	
	4–3 Total		**4.0 (8.5)**		**1.6 (3.4)**
Left	4–4	1.0 (5.6)		1.6 (1.9)	
Right	4–4	1.9 (3.5)		2.5 (3.6)	
	4–4 Total		**1.4 (4.7)**		**2.0 (2.9)**
Left	3–4	4.0 (5.4)		3.9 (6.1)	
Right	3–4	1.2 (4.2)		1.5 (2.7)	
	3–4 Total		**2.7 (5.0)**		**2.4 (4.4)**

**A state anxiety difference score was calculated by subtracting state anxiety 2 from state anxiety 1 scores. A higher score indicates a larger reduction, between ToH1 and ToH2.*

significantly longer to move the first disk). There was no significant main effect of number of disks $F(1,195) = 0.81$, $p = 0.37$. There was a significant interaction between gender and handedness $F(1,195) = 3.9$, $p = 0.05$. *Post hoc* analyses (Tukey) showed that female left-handers took longer to start than male left-handers ($p = 0.003$), and also both male ($p < 0.001$) and female ($p = 0.004$) right-handers. There were no other significant interactions.

Initiation time on second tower (novelty and complexity)

For initiation time during the second tower, there was once again a significant main effect of hand preference $F(1,195) = 6.8$, $p = 0.01$, partial $\eta^2 = 0.03$, observed power = 0.7 (with left-handers taking significantly longer to move the first disk). There was also a significant main effect of number of disks $F(1,195) = 16.4$, $p < 0.001$, partial $\eta^2 = 0.1$, observed power = 1, with a longer mean initiation time for the 4-disk task. There was no main effect of novelty $F(1,195) = 1.1$, $p = 0.29$. There were no significant interactions.

INITIATION TIME DIFFERENCES (INFLUENCE OF CONDITION)

A 2 (hand preference) × 4 (condition) between subjects ANOVA was then used to investigate the mean difference in initiation time between the first and second ToH trials. There was a significant main effect of hand preference $F(1,195) = 6.3$, $p = 0.013$, partial $\eta^2 = 0.03$, observed power = 0.7 (with left-handers having a significantly larger reduction in initiation time between trials). There was a significant main effect of condition $F(3,195) = 3.6$ $p = 0.014$, partial $\eta^2 = 0.05$, observed power = 0.8, but individual pairings were not significantly different from each other. There was also a significant interaction between hand preference and condition, $F(3,195) = 3.2$, $p = 0.026$, partial $\eta^2 = 0.05$, observed power = 0.7. Follow-up testing demonstrated that for right-handers there was no influence of condition $F(3,113) \leq 1$, but for left-handers there was a significant effect of condition $F(3,82) = 3.7$, $p = 0.015$, partial $\eta^2 = 0.1$, observed power = 0.8. As the largest initiation time differences was for the 3–3 condition (easiest task completed twice), Tukey *post hoc* tests indicated that there were significant initiation time score differences between the **3–3** and 4–4 ($p = 0.019$) and between the **3–3** and 3–4 ($p = 0.031$) conditions. No other comparisons were significant.

TRAIT ANXIETY

The mean trait anxiety score for left-handers was 40.6 and was 40.4 for right-handers. A 2 (gender) × 2 (handedness) ANOVA revealed no significant main effects or interactions.

PERFORMANCE

Performance on the Tower of Hanoi was examined using a 2 (gender) × 2 (handedness) ANOVA. There were no main significant effects of handedness or gender on number of moves or completion time for either first or second trial, but there was a handedness × gender interaction on the number of moves during the first trial [$F(1,199) = 5.0$, $p = 0.026$, partial $\eta^2 = 0.03$, observed power = 0.6). However *post hoc* tests failed to reveal any differences between the combinations.

RELATIONSHIP BETWEEN HAND PREFERENCES STRENGTH, ANXIETY, INITIATION TIME AND PERFORMANCE

As Lyle et al. (2013) found that strength of handedness was related to degree of anxiety (this relationship was only found for right-handers); it was decided to explore the inter-relationship between variables. The analysis presented here is focussed on the first tower, as this is where novelty, complexity and anxiety were easiest to compare. However, the same analysis was also done for the second tower and this is shown in **Table 5**.

Table 3 outlines the relationship between the variables strength of hand preference, initiation time, number of moves and both state and trait anxiety. This was also carried out separately for hand-preference category and gender. For brevity, analysis will focus on correlations of 0.2 or above, as well as those common and/or divergent across the data set. It is noted that although these are significant, most of these are fairly weak correlations. As would be expected, there was a significant positive correlation between number of moves and time to solve, as well as a positive correlation between initiation time and time to solve. For left-handers, there was a negative correlation between state anxiety and number of moves ($r86 = -0.245$, $p = 0.023$), suggesting that a higher level of anxiety led to a lower number of moves in solving the tower. Right-handers showed no such relationship. In terms of gender, number of moves and time to solve was also positively correlated, but male initiation time and time to solve were not. Females also demonstrated a significant negative correlation between handedness score and initiation time, showing that an increasing strength of left-handedness was related to a slower initiation time. Also, females had a positive relationship between trait anxiety and number of moves, with increasing anxiety scores related to a larger number of moves. Contrary to expectations based on Lyle et al. (2013), there was no relationship between strength of handedness and either state or trait anxiety. However, this could be due to the fact that strength of handedness in the current study was treated as a continuous variable while Lyle et al. (2013) treated this variable dichotomously in to inconsistent and consistent categories for both left- and right-handers.

A similar set of relationships were found across the second tower, except that initiation time had a stronger relationship with hand preference score (−0.245) and this was largely driven by females (−0.327). Left-handers also showed a relationship between initiation time and state anxiety in the second trial (0.266).

Potentially one of the main relationships of note was the expected positive correlation between Trait and State Anxiety, which was significant across all data sets, for both towers. However, for left-handers in the first tower the relationship was a lot weaker and it was found to be significantly different from the right-handed score ($z = -2.57$, $p = 0.01$). Females also had a lower correlation, but this was not significant. In order to better understand this, it was decided to further investigate the state and trait correlation split by both handedness and gender.

Table 4 demonstrates that all hand and gender combinations have a significant relationship between state and trait anxiety, except for left-handed females who show no such relationship. However, in the second tower, they now show

Table 3 | Correlations between main variables, for Tower of Hanoi task irrespective of disk number.

Tower 1 – All	Number of moves	Time to solve	Handedness score	State anxiety	Trait anxiety
Initiation time	−0.033	**0.223****	−0.152*	0.099	−0.043
Number of moves		**0.748****	−0.051	−0.057	0.157*
Time to solve			0.038	0.106	0.157*
Handedness score				−0.060	−0.009
State anxiety					**0.534****
Left-handers ($N = 86$)					
Initiation time	−0.163	**0.243***	0.108	0.189	−0.062
Number of moves		**0.704****	−0.164	**−0.245***	0.096
Time to solve			−0.019	0.000	0.138
Handedness score				0.015	−0.060
State anxiety					**0.370****
Right-handers ($N = 117$)					
Initiation time	0.106	**0.249****	−0.010	−0.025	−0.036
Number of moves		**0.783****	−0.096	0.082	0.198*
Time to solve			−0.035	0.183*	0.169
Handedness score				0.097	0.081
State anxiety					**0.641****
Males ($N = 93$)					
Initiation time	−0.012	0.138	−0.024	−0.007	0.091
Number of moves		**0.759****	0.090	−0.136	0.061
Time to solve			0.162	−0.008	0.118
Handedness score				0.032	0.102
State anxiety					**0.601****
Females ($N = 110$)					
Initiation time	−0.044	**0.244***	**−0.218***	0.139	−0.138
Number of moves		**0.752****	−0.161	0.018	**0.238***
Time to solve			−0.050	0.190*	0.174
Handedness score				−0.137	−0.089
State anxiety					**0.471****

**Correlation is significant at the 0.05 level (two-tailed). **Correlation is significant at the 0.01 level (two-tailed).*

a significant correlation (0.374). This suggests that on the first trial of the Tower of Hanoi they were reacting differently.

A final analysis was conducted, dividing Trait anxiety in High and Low (by use of a median split), whereby those above the median (39) were included in the former category. Each sex by handedness category was compared individually using an independent t-test. Full details are shown in **Table 6**. In nearly all cases there was a significant difference between High and Low trait anxiety groups, where the High groups showed significantly higher mean state anxiety in both towers ($p = 0.004$ or lower). The exception was for female left-handers and on the first tower only. The mean for the High Trait groups' state anxiety was 38.5 (SD = 9.8) but was 37.6 (SD = 7.8) the Low Trait group, this meant that they were not significantly different on state anxiety, $t(45) = 0.360$, $p = 0.720$. On the second trial, the High group was now significantly higher ($m = 37$) compared to the Low group ($m = 31.3$), $t(45) = 2.12$, $p = 0.039$.

DISCUSSION

It was hypothesized that state anxiety would be higher in left-handers on the first Tower of Hanoi trial only. The first hypothesis was not supported, as there was no overall significant state anxiety difference between left- and right-handers on the first ToH trial. However, there was a significant interaction between handedness and the number of disks which was influenced by the higher state anxiety levels of left-handers when they did the 3-disk Tower of Hanoi. When left- and right-hander's state anxiety levels were examined on the second ToH trial there were no significant differences between them. It was also hypothesized that initiation times would be longer for left-handers on the first ToH trial only. Left-handers took significantly longer to move

Table 4 | Correlation between State and Trait Anxiety, split by gender and hand preference.

	ToH1						ToH2	
	All	*N*	3-Disk	*N*	4-Disk	*N*	All	*N*
Female left-handers	0.073	47	0.052	23	0.057	24	0.374**	47
Male left-handers	0.617**	39	0.603**	19	0.613**	20	0.657**	39
Female right-handers	0.689**	63	0.697**	36	0.709**	27	0.641**	63
Male right-handers	0.592**	54	0.427*	26	0.672**	28	0.655**	54

**Correlation is significant at the 0.05 level (two-tailed). **Correlation is significant at the 0.01 level (two-tailed).*

the first disk on the task than right-handers, however, we also found that left-handers took significantly longer to move the first disk on the second trial therefore this hypothesis was not supported. Additionally, for all groups in the second trial the initiation times were significantly faster. When taking the complexity of the Tower of Hanoi in to consideration it was hypothesized that state anxiety levels would be higher in left-handers when completing a more complex task. This hypothesis was not supported as the highest state anxiety was found in left-handers during the 3-disk task. However, there was a significant influence of complexity on state anxiety when the four conditions were examined. The largest reduction in state anxiety occurred when participants completed the simplest task (3–3) for the second time. There was also a general handedness effect with left-hander's showing a significant reduction in state anxiety levels on the second ToH.

We also hypothesized that initiation time would be longer for left-handers when completing a more complex version of the ToH. This hypothesis was not directly supported, as initiation time was not influenced by the number of disks. However, there was a significant interaction between gender and handedness. Female left-handers took longer than the other groups to begin the task. There was still a significant main effect of handedness on the initiation time on the second task, but not for gender. As before there was a main effect of handedness across all conditions.

Although task novelty strongly contributed to left-handers' delay in initiation, it was still found (but to a lesser degree) on the second trial. This supports the view that left-handers are more behaviorally inhibited than right-handers (Wright et al., 2009) but also suggests that the nature of the task, in particular novelty and difficulty, may have an effect. The significant handedness $\times$ disk condition effect on changes in initiation time supports this view. For left-handers, the simplest task combination (3–3) had the largest drop in initiation time, and this was larger compared with when the second task complexity increased (3–4), and also when the combination was most difficult (4–4). This indicates that for left-handers, initiation time is sensitive to task complexity; when the task is not novel and simple, their initiation time is fastest.

Looking at behavioral inhibition differences, we have again shown that left-handers take longer to start a task, and this is most pronounced when the task is novel. This concurs with our previous finding on the 3-disk Tower of Hanoi (Wright et al., 2004) and a card-sorting task (Wright and Hardie, 2012) and follows expectations based on linking the right-hemisphere to inhibition and behavioral avoidance (Davidson, 1992, 1998; Sutton and Davidson, 1997). Similarly, in the context of a memory test, Lyle et al. (2012) found left-handers to be slower to respond but not less accurate. At least as far as novel situations are concerned, left-handers seem to pause longer than right-handers, but in the present case this did not have any direct influence on their performance on the Tower of Hanoi.

This supports the view that the longer initiation time is not taken up by planning the task, and that it is more likely to be a handedness related difference in assessing the situation (Piper et al., 2011). Further support may be gained from an examination of effects. Females tended to take longer to start, and female left-handers took longer than all other groups, and although it has been suggested that females are poorer at visuo-spatial tasks than males, it has also been proposed that gender does not significantly influence performance differences on the ToH (e.g., Salnaitis et al., 2011). Once again, the fact that females were not any worse in actual performance suggests that gender may be influencing performance style rather than ability to solve the task. For example, Hugdahl et al. (2006) used fMRI during a 3-D mental rotation task and found that males and females differ in terms of the processing strategies they use, with females using a verbal (language guided) approach contrasting with the perceptual (spatially guided) approach used by males. Although not tested in the present study, it remains possible that both left-handers and females may approach the solving of the task in a different way from males and right-handers.

On the other hand, the lack of a clear-cut anxiety difference was not expected as we had previously shown that left-handers exhibited a higher level of state anxiety (Wright and Hardie, 2012). Surprisingly, the first presentation of the simple (3-disk) tower elicited the highest level of state anxiety, which was shown by left-handers. The absence of a gender effect in anxiety is not surprising given the lack in previous studies where handedness was a major factor (e.g., Merckelbach et al., 1989; French and Richards, 1990; Wright and Hardie, 2012) but is in contrast to some other studies, including McLean and Anderson's (2009) review, which showed females having a higher level of anxiety. The issue of anxiety and gender will be further considered when we examine the relationship between state and trait anxiety.

In common with the developers of STAI (Spielberger et al., 1983), numerous studies have found a positive correlation between state and trait anxiety (e.g., Abdel-Khalek, 1989; Carstensen et al., 2000; Vigneau and Cormier, 2008). Lyle et al. (2013) examined anxiety during a break from testing while carrying out a cognitive task (i.e., not immediately anxiety provoking) and found a strong positive correlation (0.80) across their balanced sample of left- and right-handers. However, they do not present data for handedness classes separately. In our previous research (Wright and Hardie,

Table 5 | Correlation between main variables, for second task irrespective of disk number.

Tower 1 – all	Number of moves	Time to solve	Handedness score	State anxiety	Trait anxiety
Initiation time	**0.204***	**0.313****	**−0.245****	0.094	−0.031
Number of moves		**0.652****	−0.028	0.036	−0.041
Time to solve			0.020	0.126	−0.030
Handedness score				−0.007	−0.009
State anxiety					**0.589****
Left-handers (*N* = 86)					
Initiation time	0.188	**0.418****	−0.071	**0.266***	0.099
Number of moves		**0.762****	0.050	0.010	0.071
Time to solve			0.108	0.183	0.136
Handedness score				0.047	−0.060
State anxiety					**0.495****
Right-handers (*N* = 117)					
Initiation time	**0.240****	**0.230***	−0.099	−0.139	**−0.210***
Number of moves		**0.584****	0.107	0.049	−0.105
Time to solve			0.124	0.089	−0.127
Handedness score				0.087	0.081
State anxiety					**0.645****
Males (*N* = 93)					
Initiation time	**0.301****	**0.402****	−0.103	0.104	0.154
Number of moves		**0.527****	−0.126	0.011	−0.056
Time to solve			−0.008	0.098	−0.004
Handedness score				−0.008	−0.008
State anxiety					**0.651****
Females (*N* = 110)					
Initiation time	0.145	**0.259****	**−0.327****	0.078	−0.153
Number of moves		**0.803****	0.040	0.045	−0.037
Time to solve			0.051	0.154	−0.065
Handedness score				−0.122	−0.089
State anxiety					**0.540****

**Correlation is significant at the 0.05 level (two-tailed). **Correlation is significant at the 0.01 level (two-tailed).*

2012) immediately after participants received the instructions for a computerized cognitive task (i.e., an anxiety provoking situation), we found that for both left- and right-handers, state and trait anxiety were significantly positively correlated (0.55 overall, with 0.57 for left-handers and 0.51 for right-handers). Gender and handedness were not separately presented in the original study, but re-analysis of the raw data has shown that female left-handers did not have a significant correlation between state and trait anxiety, while the other three groups did. This data was from a different sample from the present study, and suggests that in a novel and stress-inducing situation, left-handed females appear to show a state anxiety response that is not immediately related to their trait anxiety levels. Some support for females occasionally showing this kind of disconnection, comes from a study into maths anxiety, where females but not males had a mismatch between their state and trait anxiety levels (Goetz et al., 2013).

State anxiety has been shown to be a good measure of current anxiety, as it can chart differences in response before, during and after a stressor is presented (Harrigan et al., 1991). It also corresponds to experimental manipulations that either increase stress (e.g., lecturing to 200 people; Filaire et al., 2010) or decrease stress (e.g., using Yoga to relax; Subramanya and Telles, 2009). State anxiety itself may consist of two components, 'worry' and emotionality and the latter is considered to be equivalent to neuroticism (Mellanby and Zimdars, 2011). However, worry is thought to be the component that may influence performance (Hayes et al., 2008) and while in the current study there were no obvious performance effects, left-handers had the highest level of state anxiety on their first 3-disk task along with the longest initiation time. In all cases left-handers had the longest initiation time, but this was not always associated with a higher level of state anxiety. Thus, the relationship between handedness, anxiety and performance on the Tower

Table 6 | Influence of trait anxiety category (high versus low) on State anxiety levels for both towers.

	Female left handers	Male left handers	Female right handers	Male right handers
Tower 1				
High trait anxiety	38.5 (9.6)	38.9 (8.7)	39.7 (7.8)	39.1 (10.4)
Low trait anxiety	37.6 (7.8)	30.7 (9.4)	30.0 (7.2)	31.1 (7.8)
Independent-*t*	0.360	2.8	5.1	3.2
p-value	0.720	0.008	<0.001	0.002
Tower 2				
High trait anxiety	37.0 (9.4)	33.3 (6.4)	36.8 (8.8)	36.5 (10.0)
Low trait anxiety	31.3 (8.8)	27.1 (6.3)	25.9 (5.6)	27.8 (6.0)
Independent-*t*	2.1	3.1	5.7	3.9
p-value	0.039	0.004	<0.001	<0.001

of Hanoi is complicated, influenced by novelty, complexity and gender.

In contrast, trait anxiety may be a good predictor of general responsiveness (e.g., Bishop et al., 2004). For example, high trait anxiety has been linked with risk-avoidant decision-making (Broman-Fulks et al., 2014) but it may not be sensitive to changes in current stressors (e.g., Cesci et al., 2009). Trait anxiety is also thought to be a predictor of propensity to react in a vigilant and threat seeking manner (e.g., Mathews and McLeod, 2002) and as such, has been used a predictor of responsiveness. For example, trait anxiety differences (usually categorizing participants into a high versus low trait anxiety group) have been successfully used to predict between group differences in a number of tasks (Koster et al., 2005; Viaud-Delmon et al., 2011). Schlotz et al. (2006) showed that an association between cortisol and subjective performance pressure was mediated by trait anxiety – with no association at low levels but thereafter it was higher as trait anxiety increased. Trait anxiety also correlates with neuroticism (Luteijn and Bouman, 1988), so the degree that each measure is tapping into something different may be unclear, but theoretically the 'worry' aspect of state anxiety may best reflect the component of anxiety that is most strongly influenced by the current situation. In any case, as Wilt et al. (2011, p. 989) put it 'Although trait anxiety may influence the level or probability of state anxiety, it is likely that trait and state forms of anxiety are not completely isomorphic; that is, trait and state anxiety may arise from different causes and have different consequences.'

Linking anxiety and behavior to the revised reinforcement sensitivity theory (rRST) may provide some additional clues. Wright and Hardie (2011) have proposed a link between handedness and degree of Behavioral Inhibition, in the context of Gray and McNaughton's (2000) rRST. This theory describes personality in terms of three major interacting systems that influence action (Corr and McNaughton, 2008), and these are the behavioral activation system, or BAS, the fight-flight-freeze system (FFFS), and the behavioral inhibition system (BIS). Full details of the systems are provided elsewhere (Corr, 2008). Briefly, BAS relates to approach behavior, covering impulsivity and novelty seeking which is thought to underpin approach behavior and FFFS covers responses to aversive stimuli, mainly via avoidance, either defensive (fear) or escape (panic). In this revised model, BIS takes on the role of conflict resolution, and is activated whenever there is a conflict going on. This conflict may involve conflict goals between the systems (e.g., BAS– approach and FFFS – avoidance) or within a system and BIS inhibits on-going action, focuses resources and attention toward the object of the conflict, and crucially brings in the emotive response of anxiety. In terms of handedness, we have argued (Wright and Hardie, 2012) that as left-handers score themselves higher on BIS scales, but there are no hand-preference differences on the other scales, then this may hold the key to understanding behavioral differences. Supporting the role of BIS as a conflict resolution system, Smillie et al. (2007) found that measures of BIS-reactivity predicted increased response-sensitivity and response bias in goal conflict situations. In addition, BIS sensitivity is linked to a preference for familiarity, where high BIS is associated with a stronger preference for familiar images (Quilty et al., 2007). BIS is also positively associated with self-reported emotional regulation difficulties (Tull et al., 2010), suggesting that it relates to anxiety and rumination. It is important to note that anxiety serves as a mechanism to focus attention toward the conflict (Corr, 2011). BIS activation inhibits ongoing behavior, thus causing a pause in proceedings, while simultaneously directing arousal and attention toward the stimuli causing the conflict, resulting in a state of anxiety. In this context, anxiety operates as an emotional state that seeks to resolve the conflict, and is experienced in the form of worry and rumination about the source of the conflict, which increases until the point of resolution (see Corr and McNaughton, 2008). This resolution can be either an approach or avoidance. In the present case, the resolution to the conflict would be the start of the tower task, namely initiating the task, so rRST may be an explanation for the general tendency for left-handers to take longer to start a novel task.

A general difference in responsiveness between left- and right-handers is also supported by studies looking at physiological responsiveness to physical stressors. For example, Jaju et al. (2004) found in males, that when performing the cold pressor and handgrip dynamometry tests with their preferred hands, that the heart rate increase from baseline levels was significantly greater for left-handers. This suggests a possible difference in left and right-handers in their autonomic control over their cardio-vascular systems. When mental stress (i.e., cognitive load) is added in the form of a mental arithmetic task, measurement of vascular reactivity (comparing the increase from baseline to cognitive load condition) was significantly greater for left-handers including both males and females (Stoyanov et al., 2011). This suggests that when left- and right-handers are placed into stressful situations, that left-handers may show a relatively larger increase in physiological responsiveness than right-handers. However, these explanations do not fully explain all the current findings, especially the response of female left-handers on their first trial.

An alternative, or related, explanation for the state and trait anxiety findings, particularly those related to both simplicity and gender is the concept of stereotype threat or priming. Stereotype threat can be defined as an action which affects performance due to the influence of a stereotype about a specific group (Hively and El-Alayli, 2014). This is often a negative action (and can be detrimental to performance) but can also be positive (and enhance performance). The most widely cited stereotype threat literature focuses on gender stereotypes.

Research examining the relationship between anxiety and stereotype threat has found mixed results. Some studies report that self-reported anxiety is not related to performance in a stereotyped group (e.g., Schmader, 2002) while other findings show that anxiety significantly influences performance (e.g., Osborne, 2001). Bosson et al. (2004) examined different types of anxiety in relation to stereotype threat and found that those in a stereotype threat situation demonstrated more non-verbal anxiety than self-report anxiety. In addition, females' self-reported maths anxiety was found to be influenced by gender stereotypes about maths (Goetz et al., 2013). In our study we did find that the left-handed females reported significantly higher levels of state anxiety when faced with a simple task. Although this appeared to influence their approach it was not detrimental to task performance.

The positive or negative effect of the stereotype priming on cognitive performance depends whether the participant views the testing session as challenging (Hausmann, 2014). In our study when left-handed females view the 3-disk ToH for the first time it contains two main pieces of information. The first is that it is a simple task; there are three pegs and 3-disks. The second piece of information is that it is a visuo-spatial task; participants have to move single disks through space and put them on alternative pegs until the task is solved. It is a well-known finding that males tend to outperform females on visuo-spatial tasks and are more confident in their cognitive abilities (Hausmann, 2014). Additionally females have been found to perform worse on spatial tasks when contextualized in a stereotype threat manner (i.e., informing females that they do not perform this type of task as well as males, e.g., McGlone and Aronson, 2006). Therefore we could argue that in our study, females, in general would have higher levels of state anxiety when asked to complete the ToH (which they did). However, to try to explain why *left-handed females* have the highest state anxiety levels it is proposed that the simplicity of the task could be influencing this. The 3-disk ToH is a relatively simple task, therefore the possibility of failure or not solving the simple task efficiently could influence the state anxiety levels of the left-handers. Conversely the 4-disk ToH, looks relatively more complex and thus it could be argued that the pressure to perform the task efficiently is reduced (as it is expected that it is complex and thus a minimum moves solution would be much more difficult to obtain). The level of stereotype threat could also be influenced by social factors such as people's perceptions of performance. Therefore state levels of anxiety could be influenced by the presence of the experimenter who is observing the performance on the task.

Left-handers as a group are potentially susceptible to stereotype threat. There are many negative associations cited which could cause left-handers to become more aware of the situation and this in turn could influence both anxiety levels and task performance. Many left-handers have grown up hearing about negative connotations such as left-handedness is pathological (Satz et al., 1985), left-handers are more likely to display symptoms of depression (Denny, 2009) or left-handers have lower levels of intelligence (Hicks and Beveridge, 1978). Adding to this is popular science literature such as 'the left-hander syndrome' (Coren, 1993) and 'Handedness and developmental disorder' (Bishop, 1990). Spere et al. (2005) showed a putative link between handedness and self-consciousness, where right-handed individuals tended to have lower levels of self-consciousness, although this was only approaching significance. To date there is no literature investigating stereotype threat in left-handers but we propose that it is an interesting concept which needs to be further investigated.

LIMITATIONS

For links to rRST, it is important to note that we did not measure BIS and future work should measure this within the context of the work, rather than rely on associations from other work. The number of participants is another limitation, as having four conditions and gender as variables there were insufficient numbers of female left-handers in the sample to allow the results to be even more finely investigated.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 20 October 2014; accepted: 12 January 2015; published online: 03 February 2015.

Citation: Wright L and Hardie SM (2015) Left-handers look before they leap: handedness influences reactivity to novel Tower of Hanoi tasks. Front. Psychol. ***6****:58. doi: 10.3389/fpsyg.2015.00058*

This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology.

frontiers in Psychology

ORIGINAL RESEARCH
published: 28 August 2015
doi: 10.3389/fpsyg.2015.01203

Are there right hemisphere contributions to visually-guided movement? Manipulating left hand reaction time advantages in dextrals

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OPEN ACCESS

Edited by:
Claudia L. R. Gonzalez,
University of Lethbridge, Canada

Reviewed by:
Jody L. Jensen,
University of Texas at Austin, USA
Liana Brown,
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Specialty section:
This article was submitted to Movement Science and Sport Psychology, a section of the journal Frontiers in Psychology

Received: 24 December 2014
Accepted: 29 July 2015
Published: 28 August 2015

Citation:
Carey DP, Otto-de Haart EG, Buckingham G, Dijkerman HC, Hargreaves EL and Goodale MA (2015) Are there right hemisphere contributions to visually-guided movement? Manipulating left hand reaction time advantages in dextrals. Front. Psychol. 6:1203. doi: 10.3389/fpsyg.2015.01203

Many studies have argued for distinct but complementary contributions from each hemisphere in the control of movements to visual targets. Investigators have attempted to extend observations from patients with unilateral left- and right-hemisphere damage, to those using neurologically-intact participants, by assuming that each hand has privileged access to the contralateral hemisphere. Previous attempts to illustrate right hemispheric contributions to the control of aiming have focussed on increasing the spatial demands of an aiming task, to attenuate the typical right hand advantages, to try to enhance a *left hand* reaction time advantage in right-handed participants. These early attempts have not been successful. The present study circumnavigates some of the theoretical and methodological difficulties of some of the earlier experiments, by using three different tasks linked directly to specialized functions of the right hemisphere: bisecting, the gap effect, and visuospatial localization. None of these tasks were effective in reducing the magnitude of left hand reaction time advantages in right handers. Results are discussed in terms of alternatives to right hemispheric functional explanations of the effect, the one-dimensional nature of our target arrays, power and precision given the size of the left hand RT effect, and the utility of examining the proportions of participants who show these effects, rather than exclusive reliance on measures of central tendency and their associated null hypothesis significance tests.

Keywords: cerebral asymmetry, reaching, handedness, visuospatial processing, attention, reaction time

Introduction

The idea of a specialized role for the left hemisphere in the control of movement is well-established in the neuroscience literature (Kimura and Archibald, 1974; Paillard, 1982a,b; Goodale, 1988; Kimura, 1993; Elliott and Roy, 1996; Rothi and Heilman, 1997; Goldenberg, 2013). Nevertheless, surprisingly few investigations have examined the relative contributions of the two hemispheres to the programming and control of movement. One approach to this question has been to contrast differences in the movements made by groups of unilateral brain-damaged patients. To date, however, little consensus has been reached in these experiments, except for the general tendency for right-brain damaged (RBD) participants to initiate their movements more slowly than their left-brain damaged (LBD) counterparts (Fisk and Goodale, 1988; Haaland and Harrington, 1989, 1996). This result (and similar results from the hand difference literature using neurotypical participants, see below) is usually interpreted in terms of some sort of right-hemisphere process that is important for: (1) localizing a target in space; (2) shifting or allocating attentional resources; or (3) "premotor processing" [the latter tends mainly to refer to any processes related to the reaction time (RT) period].

Inferences derived from deficits following brain damage, on their own, can be difficult to interpret unambiguously (Kosslyn and Intrilligator, 1992; Shallice and Cooper, 2011). Hypotheses about hemispheric contributions to movement would be strengthened if they were supported by independent evidence from other research domains. One such domain is the study of hand differences in neurologically-intact participants. Given the "privileged access" of each hand's motor outflow and sensory inflow to other mechanisms in the contralateral hemisphere, subtle differences in the performance of the left and right hands should, in theory, be consistent with the specializations of each hemisphere (e.g., Goodale, 1988, 1990; Poizner et al., 1990; Bagesteiro and Sainburg, 2002). One result, commonly reported in the visually-guided aiming literature, is that left-handed movements are initiated more quickly (e.g., Carson et al., 1992; Carson, 1996), while right-handed movements are completed more quickly once initiated (e.g., Elliott et al., 1993, 1994).

Of course, the majority of hand performance studies have investigated right-handed participants and reported advantages for the right hand. The most robust of these advantages is **a** shorter dominant hand movement duration (Fisk and Goodale, 1985; Carson et al., 1993a,b; Elliott et al., 1994). Accuracy usually favors the right hand as well, suggesting that these shorter movement times (and higher peak velocities) are not an obvious result of a speed-accuracy trade off, at least for these measures of speed.

A potentially more promising approach than simply documenting any obtained hand difference, has been to manipulate task demands in some fashion and make one-tailed, directional predictions about shifts away from advantages for a specified hand in right-handed participants (Watson and Kimura, 1989; Carson et al., 1990, 1992; Elliott et al., 1993). Three such studies are reviewed in detail by Carson (1996). Effectively, most of these studies have manipulated some feature related to the target of an aiming movement, which was thought to increase the spatial demands of the task.

For example, Carson et al. (1992) had participants extrapolate from a spatio-temporal pattern of targets to determine a reach endpoint which completes the figure. Four such figures were used, which depicted linear, quadratic, cubic, and quartic functions. The assumption made by the authors was that the number of "reversals" in a pattern predicted the spatial complexity-linear the least spatially complex, quartic the most spatially complex. The authors did not find the expected differences as a function of target.

Other published attempts at increasing the spatial complexity of an aiming task which have been investigated include interpolating the center of circles of different sizes (Elliott et al., 1993, experiment 1), reaching quickly and accurately to one of two different types of targets in one of two different locations (Elliott et al., 1993, experiment 2); and pointing to the mirror image of a target's location (Chua et al., 1992). Although the stimuli used in such tasks are plausible as spatially complex in some respects, the tasks that the participants are required to complete may not be. For instance, in some of the tasks participants actually had to reach to an identical position for each of the different targets (Carson et al., 1992; Elliott et al., 1993). In Elliott et al. (1993), for example, the circles of different diameters were always centrally positioned on paper backgrounds which required identical movement amplitudes to point to their centers.

Specific methodological details aside, these approaches tend to make broad assumptions about what constitutes a spatial manipulation. Unfortunately to date they also tend not to work (in terms of increasing or attenuating left hand RT advantages). In fact, many of the null effects of task in these experiments led Carson (1996) to conclude that any right hemispheric contributions to left hand reaction time advantages "do not arise from an engagement in spatial co-ordinate processing" (p. 163). In other words, Carson argues that whatever mechanisms drive the left hand RT advantage, they don't seem to relate to visuospatial processes.

In the current study, we explored the hypothetical right hemispheric driver of the left hand RT advantage with three different experiments. Our main aim was to identify a manipulation which would affect the size of the left hand RT advantage, providing more direct evidence that this hand difference is a consequence of a right hemisphere process. For two of the tasks, we were motivated by independent evidence suggesting right hemispheric specialization, in experiment 1 (bisection) and experiment 3 (the gap effect). This latter study also constituted a more direct test of an attentional, rather than a strictly visuospatial, contribution to the left hand RT advantage, rarely done before (see Mieschke et al., 2001 for a noteworthy exception). For the remaining task, we attempted to manipulate spatial processing by altering the number of potential targets (experiment 2). In our first experiment, we attempted to circumvent the difficulties associated with defining spatial complexity using the old-fashioned approach of avoiding it altogether, by using a task with a known right hemispheric specialization (i.e., bisection of the space between two targets).

In all of the studies described below, participants were encouraged to make quick and accurate movements, but after early testing in one of our labs, we elected to emphasize speed more than accuracy in subsequent experiments where non-dominant hand performance was assessed alongside dominant hand performance. Occasionally participants are concerned (often unjustifiably so) about performance of their "weaker" hand, so would adopt a more conservative strategy by slowing down in practice trials.

Experiment 1: Single-target Pointing vs. Two-target Bisecting

The present study attempted to investigate right hemispheric contributions to visually-directed aiming by using a task which is strongly linked to right hemisphere specialization–bisection. Evidence from many clinical and experimental studies links poor performance on bisection of lines with right hemisphere damage. Paper and pencil line bisection frequently reveals neglect of left space in participants with RBD, as participants place their "mark" too far to the right (e.g., Schenkenberg et al., 1980; Milner et al., 1993). Additionally, it has been shown that in a task which was a visuomotor variant of line bisection, RBD patients who had recovered from hemispatial neglect performed more poorly than left-brain damaged patients. Thus, when the terminal endpoint for an aiming movements was defined by the perceived midpoint of two LEDs, RBD patients erred to the right, even though they were able to correct rightward deviations in the initial portion of reaches made directly to single LEDs (Goodale et al., 1990).

The aim of the present experiment was to determine whether it is possible to exaggerate the magnitude of the left hand RT advantage, therefore providing some evidence to support the hypothesis that this effect is driven by a right hemispheric specialization. In order to do so, we required participation in both a standard aiming task and a bisecting task, where the correct endpoints were co-incident in both. If accurate performance in bisection is more reliant on the right hemisphere than in single-target pointing, a left hand advantage in RT should be stronger in this condition. A second factor manipulated was the visibility of the hand during the reaching movement (also see Carson et al., 1992). Some studies have suggested that proprioception/kinesthesis may rely more heavily on right hemispheric systems (e.g., Guiard et al., 1983; Carson et al., 1990). If this hypothesis is correct, then any attenuation of right hand advantages in bisecting may be exaggerated in hand-invisible reaching.

Methods

Participants

Fourteen strongly right-handed males were tested. These volunteers were research assistants, graduate students and senior undergraduates from the University of Western Ontario. Participants completed a nine-item handedness questionnaire (a modified version of the Edinburgh Handedness Inventory; Oldfield, 1971) and were included in the study only if they performed all nine actions with their right hand. Participants ranged in age from 19 to 30 years (mean = 24.5).

Procedure

Participants were required to reach quickly and accurately toward targets under two different hand visibility conditions, run on separate days; one in which the reaching limb was visible and the other in which the limb was not visible. Session was counterbalanced. Both hands were tested on each day, and the order of hand and task was also counterbalanced.

Participants pointed to single targets, or "bisected" two targets, in 30-trial blocks. Target light-emitting diodes (LEDs; red; 0.25°) were embedded in a Styrofoam wedge, centered 2 cm from the table surface, angled toward the participant's eyes, and covered in black speaker cloth (such that the location of LEDS was not visible until they were illuminated individually or in pairs). During a session, participants wore a black long-sleeved t-shirt and a black glove on the reaching limb (in order to eliminate as much as possible any visual cues from the limb during hand-invisible reaching). All calibration and test trials were performed while in a chinrest, angled to provide optimal viewing of the targets in the wedge. Small, infrared-emitting diodes (IREDs) were attached with Velcro to the tip and the base of the index finger on the glove. The three-dimensional locations of these diodes during calibration and test trials were recorded at 100 Hz using an opto-electronic recording system (WATSMART, Northern Digital, Inc.).

After collection of five calibration trials (where participants were allowed to adjust endpoint position to make perfect reaches to continuously-illuminated LEDS), participants were required to reach quickly and accurately to each presented LED target and to remain in their initial landing position until instructed to return to the start position and await the next trial. Participants were told that targets could appear anywhere on the target wedge in front of them, but were not told how many different targets would appear. Five different target positions were used (far left, near left, center, near right and far right, each 6 cm away from the adjacent target). The central target was located 32 cm in front of the start position, and the two most peripheral targets were 34 cm away from the start position (21.5° from the central target). Each target appeared six times, in a pre-determined, pseudo-random sequence.

For bisecting, participants were instructed to reach quickly and accurately to the midpoint between two simultaneously illuminated targets. The two LEDs for any particular bisecting trial were positioned 12 cm apart, and their true midpoints were located at the same positions as the five pointing targets (see **Figure 1**).

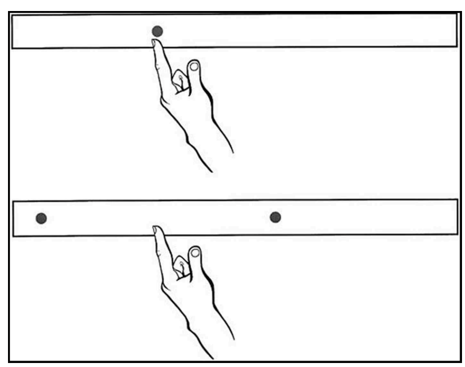

FIGURE 1 | Schematic representation of the pointing and bisecting conditions of experiment 1. Five targets/midpoints were used, equally spaced by 6 cm from a midline target/midpoint. Adapted from Goodale et al. (1990).

Data Analysis

After data collection, raw WATSMART files were converted to three-dimensional coordinates and filtered at 7-Hz with a second-order Butterworth filter. These filtered files were used to compute peak velocity (cm/s), movement onset time and movement duration (both in ms), and two different measures of endpoint accuracy (relative to the position of the fingertip LED specified by the calibration trial for that particular target/endpoint).

Each dependent measure was analyzed using three factor repeated measures analysis of variance, using the Geiser–Greenhouse adjustment of the degrees of freedom (for violations of homogeneity of covariance in repeated measures designs) when appropriate (Kirk, 1982; Tabachnick and Fidell, 1989). Significant interactions were explored using a simple main effects procedure (Kirk, 1982). The main effects and interactions relevant to hand differences in RT will be the main focus of the rest of this paper (see Supplementary Materials for statistical analyses of the other dependent measures in this and the other two experiments).

Results

The principal aim of the study was to see if left hand RT advantages in pointing would be increased by the theoretically more "right hemispheric" bisecting task relative to single target pointing. **Table 1** includes mean RT as a function of hand, task and visual feedback condition. **Figure 2** show these means separately for ipsilateral and contralateral hemispace (see Carey et al., 1996; Carey and Otto-de Haart, 2001). In only one of the four comparisons (two tasks × two hand visibility conditions) is the left hand even marginally quicker than the right. In fact, none of these differences in RT are statistically significant, even as assessed by 1-tailed paired samples *t*-tests: pointing: $t_{(13)} = 0.215$ and $t_{(13)} = -0.634$; bisecting: $t_{(13)} = -0.475$, and $t_{(13)} = 0.702$.

We also wanted to examine the proportions of these samples who show numerical left hand RT advantages. Even though these effects are small in neurologically-intact participants, if they are related to cerebral asymmetries in attentional/visuospatial processes then the majority of any right handed sample should show them (see Carey and Johnstone, 2014 for further discussion of the relevance of proportions for neuropsychological experiments comparing right- and left-handed participants). Of course, what precise proportion of dextral people who are right brain dominant for attentional of visuospatial function is not well-established, although see Cai et al. (2013) for some relevant data from fMRI. If one assumes complementary specialization of the right hemisphere when an individual is left hemisphere dominant for speech and language functions, then the proportion should be as high as 90–95%.

As suggested by the means, only one of the four conditions resulted in a majority proportion of the sample having left hand RT numerically smaller than right hand RT, which was in hand-invisible bisecting (0.64; hand-visible pointing = 0.50, hand-invisible pointing = 0.50, and hand-visible bisecting = 0.50).

Discussion

These data are fairly easy to interpret in terms of left hand RT effects. In spite of the fact that our pointing task did not result in the often obtained left RT advantage, there is no evidence for bisecting shifting left hand RTs lower in relative terms. Numerically, at least, RTs did not favor the right hand in hand-invisible bisecting, but this shift relative to hand-invisible pointing was not statistically significant, even with rather liberal

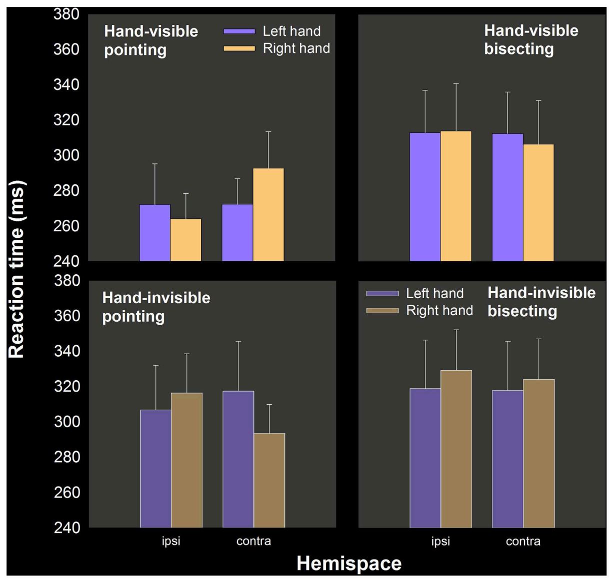

FIGURE 2 | Mean RT as a function of hand, hand visibility, hemispace, and task, experiment 1. A lower left hand RT, relative to the right hand, was only obtained in hand-invisible bisecting, but this difference was not statistically significant.

TABLE 1 | Mean RT (ms) as a function of task, hand and hand visibility.

Pointing					Bisecting			
Visible		Invisible			Visible		Invisible	
Mean	SEM	Mean	SEM		Mean	SEM	Mean	SEM
269.3	13.4	300.2	17.6	**Right**	310.2	24.5	321.7	21.5
272.2	17.4	307.2	24.1	**Left**	312.7	23.5	312.9	25.9
−2.9		**−7**		**Diff (R–L)**	**−2.5**		**+8.8**	

SEM = standard error of the mean. A positive difference score (bottom row) indicates a numerical left hand RT advantage.

one-tailed t-testing. The proportions who show left hand RT advantages did change slightly in one bisecting condition (but the sample size in this experiment is rather small for this sort of proportional analysis).

There is little evidence to suggest what conditions tend to favor RT advantages for the left hand (after all that is what these experiments were designed to ascertain), therefore occasionally null findings in a control condition such as pointing in the present study, will limit the usefulness of any attempt to manipulate hand differences in RT. Unfortunately, this one interesting measure which usually favors the left hand of the right hander, is not obtained in every experiment.

Undeterred by this first attempt, with a new sample of right handers we attempted a somewhat different type of manipulation, targeted more directly at the *localization* demands of a manual aiming task.

Experiment 2: Manipulating Localization Demands by Increasing the Number of Target Locations

One sensible way to try and quantify the relative contribution of the right hemisphere to motor control would be to keep the task focussed on the spatial localization of targets for the production of rapid movements. Localization refers to a diverse set of processes which allow for specifying the location of an external target to some sort of egocentric or body-centered representation (Bock, 1986; Miller, 1996). The evidence for a right hemisphere advantage for the localization of targets (Kimura, 1969), perhaps in relatively early stages of movement planning (Carson et al., 1992) motivated this second experiment. Here, we varied the visuospatial demands of the task by manipulating target uncertainty, while requiring identical motor responses (as in experiment 1). If a left-hand advantage for movement onset reflects right-hemispheric specialization for target localization, the expectation was that increasing the spatial uncertainty of the task by increasing the number of target locations should result in an interaction between hand used and target number of targets. We expected the largest left hand RT advantage occurring in the block with the greatest number of possible target positions. In addition, RT advantages should be decreased in the 2 target condition, relative to the intermediate 6 target condition, if target localization demand predicts left hand RT advantages.

Methods

Participants

Participants were 22 volunteers, 12 females and 10 males, mainly undergraduate and postgraduate students from the University of Aberdeen, ranging in age from 18 to 41 years (mean = 26.6, SD = 6.9). They were self-declared strong right-handers, verified by a 9-item handedness inventory (a modified version of the Edinburgh Handedness Inventory; Oldfield, 1971). All participants were naïve as to the purpose of the experiment and took part in two test sessions, one in which the right hand was tested and the other in which the left hand was tested, run on separate days.

Procedure

A 60 Hz MacReflex three camera motion capture system was used, coupled with a bespoke light emitting target board controlled by an adjacent PC. The participants were given six blocks of trials in which the number of targets used were varied. Each block's targets were symmetrical, and centered 15 cm (14.6°) to the left and right of a midline fixation point (the two targets used in block A were at these two positions; see **Figure 3**). In block B, six targets were used; inner targets were 9.8° from fixation and the outer were at 19.5°. In block C, 10 targets were used, equidistant, at 4.9° at most medial to the most lateralized at 24.2°.

The targets presented in each block appeared randomly. The blocks were run in an ABCCBA or CBAABC order, to counterbalance for any potential practice or fatigue effects. The two middle blocks (which both had either 10 targets or 2 targets) were separated by a brief delay. Half of the participants began with block A, while the other half began with block C.

In the test session a total of 144 trials were run for each hand. In each block 4 pointing movements were required, in random order, to each stimulus target used. Practice trials (one movement to each possible target) were provided in each of the first new blocks to familiarize the participant with the number and location, of the 2, 6, or 10 targets. All participants were also told the number of targets in each block verbally before the practice trials.

Results

We predicted an interaction between number of targets and hand, such that RT differences that favor the left hand should have been largest in the 10-target condition and smallest in the 2-target condition. The data, shown separated for left and right hemispace, are depicted in **Figure 4**.

A three way repeated measures analysis of variance with hand, number of targets, and hemispace was performed. Overall the hands did not differ in RT [$F_{(1, 20)} = 3.75, p = 0.067$], ipsilateral movements were initiated more quickly than contralateral movements [$F_{(1, 20)} = 27.57, p < 0.001$]. No other effects were statistically significant, including the Hand × Number of targets × Hemispace [$F_{(2, 40)} = 3.132, p = 0.054$]. Nevertheless

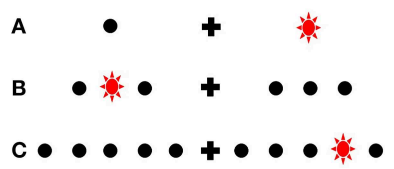

FIGURE 3 | Schematic representation of target uncertainty in experiment 2. Only two possible target positions could be illuminated in Block **(A)**, relative to the 10 possible in Block **(C)**. Note how the each array is centered equivalently relative to fixation [i.e., middle targets in **(B)** and **(C)** are aligned with the only target in each hemispace in **(A)**]. Drawing not to scale.

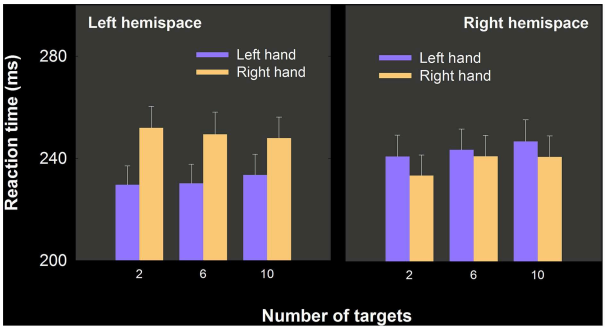

FIGURE 4 | Mean RT as a function of hand, number of targets and hemispace, experiment 2. Left hand RT advantages were significant, depended on larger ipsilateral advantages than those obtained in the right hand, but did not interact with the number of targets. Note that in each panel, we have plotted ipsilateral (i.e., left hemispace, left hand; right hemsipace, right hand) movement means before contralateral movement means.

given our directional prediction we ran three paired samples *t*-tests on the 2, 6, and 12 target blocks comparing right hand–left hand RT. The left hand RT advantage was only statistically significant for the 6 target conditions [$t_{(21)} = 2.35$, $p < 0.02$]. We also compared the proportion of the sample who showed a *numerical* left hand advantage in the 2, 6, and 10 target conditions. The resulting proportions were 0.67, 0.76, and 0.71.

A summary of results for other dependent measures appears in the Supplementary Materials.

Discussion

As in experiment 1, there was little evidence for any exaggeration of left hand RT advantages as target numbers increased from 2 to 6 to 10. In this experiment, unlike the previous one, there was at least a possibility for exaggeration or attenuation of the left hand RT effect, as most of our participants (76%) had numerical left hand RT advantages in the "intermediate" 6-target block (which in some sense is the control condition in this experiment). Nevertheless, the mean RT effect did not increase or decrease significantly across blocks, and the proportion of the sample who have numerical left hand advantages was virtually unchanged in 2-, 6-, and 10-target conditions.

Of course, targets were restricted to placement within a horizontal array, which may not have taxed systems that normally localize with eye, head and hand in a multidimensional world. Furthermore, although more target uncertainty was introduced, theoretically the attentional demands of the 2, 6, and 10 target conditions may not have differed by much; the horizontal extent of the space which may have contained targets for any block varied from 30° (2 target blocks) to 46° (6 target blocks). These two horizontal extents are well within the binocular visual fields, and may not have differed sufficiently in terms of the extent of space to be monitored for potential targets in a speeded aiming task. In fact, while we were designing this task we became well-aware of how different distances and or different spatial resolutions are necessary to vary target number—it was difficult to know how to trade these factors off with one another in the absence of any strong data on left hand RT mechanisms. In any case, this kind of thinking about attention in reaching led us to our final experiment, where we used a manipulation coupled to two somewhat distinct *attentional* mechanisms, both linked with right-hemisphere specialization, which may account for the left hand RT effect.

An additional analysis of a subset participants who showed left hand RT advantages overall, also provided no support for the hypothesis that target number influenced the magnitude of the left hand RT advantage.

Experiment 3: Fixation-target "Gap" vs. "No-gap" Pointing

In the final experiment, we attempted a manipulation directed toward a more attentional explanation of the left hand RT effect. Right hemisphere specialization for attentional systems has been suggested for some time, from studies of patients with hemispatial neglect (Brain, 1941; De Renzi, 1982; Danckert and Ferber, 2006) and neurotypical participants (e.g., Gitelman et al., 1999; Jewell and McCourt, 2000; Rushworth et al., 2001; Mattingley et al., 2004; Shulman et al., 2010; Voyer et al., 2012)[1]. Of course, in single-target aiming, two different types of attention may play roles in facilitating rapid responses. First, generalized alertness or vigilance (Marrocco et al., 1994), could be facilitated by preparing to use the left hand, largely controlled and monitored by motor, premotor and somatosensory networks of the right hemisphere (for evidence linking generalized alertness to the right hemisphere, see Posner and Peterson, 1990; Robertson et al., 1998). An alternative attentional mechanism might be related to a more spatially—selective process such as visual orienting to a target (Posner and Peterson, 1990; Petersen and Posner, 2012).

For this study, we chose a manipulation which has requirements related to both types of attentional component—the "gap effect" (Saslow, 1967). This effect refers to facilitated RTs for targets when a short delay (typically 100–200 ms) between fixation offset and target onset is introduced. Although described initially in a two-target saccadic eye movement paradigm (Saslow, 1967; Fischer and Ramsperger, 1984) a manual gap effect has also been identified, although there is some debate over whether or not the effects are carried over from saccadic facilitation (Bekkering et al., 1996). Perhaps coincidentally, the magnitude of the manual gap effect is typically around 15–20 ms (Reuter-Lorenz et al., 1991; Bekkering et al., 1996; Fendrich et al., 1999), which is not disproportionately larger than the left hand RT advantages in reaching experiments. What was crucial for our purposes was that there is some evidence that the gap effect results from *both* the general alerting effect of fixation offset (Dorris and Munoz, 1995; which takes some time to manifest itself) and from a spatial orienting/facilitation effect (e.g., attention is released from fixation which can now be allocated in the direction of a manual/saccadic target; Kingstone

[1]Surprisingly few studies report left visual field advantages in neurotypical participants for visual search and Posner-like cueing tasks; (see Palmer and Tzeng, 1990; Evert et al., 2003; Michael and Ojéda, 2005; Poynter and Roberts, 2012, for examples, caveats and analysis).

and Klein, 1993; Pratt et al., 2000; Rolfs and Vitu, 2007). In other words, this study was a first pass at an attention explanation of the left hand RT advantage, which we intended to explore if successful using manipulations from the gap effect literature designed to fractionate the alerting and orienting components.

Interestingly, there are some indications of a hemispatial asymmetry in the manual gap effect. Lünenburger et al. (2000) found a slightly larger manual gap effect when right-handers reached toward the right side of space, compared to equivalent left-sided reaches. However, as the left hand was not examined in that experiment, the conclusions that can be drawn from this finding are limited. Gomez and colleagues also found larger gap effects when dextrals had to react to targets appearing in their right visual field (Gómez et al., 1998). However, this study tested only choice reaction times (pressing left mouse button for a left target and the right mouse button for a right target), rather than manual localization, as was required here.

The current experiment includes data from three separate gap effect studies performed by GB, HCD, and DPC, which differed slightly in precise methods but all required: (1) right-handed participants to reach in gap and no gap (fixation offset coincident with target onset) conditions; (2) target arrays that were balanced with respect to the participant's midline (i.e., half in each hemispace), and (3) separate blocks of left and right hand unimanual reaches, made as quickly (and accurately) as possible.

Methods

Participants

A total of 67 participants were tested over the course of the 3 experiments (26 in study 1, 21 in study 2 and 20 in study 3). The mean age of the samples was 22.0 years, SD = 2.83. All participants had normal or corrected to normal vision. All participants were dextral, with strength of hand preference measured by a modified version of the Waterloo Handedness Questionnaire (WHQ; Steenhuis and Bryden, 1989; mean = 26.85/30; SD = 3.48). Participants were naïve to the hypothesis (including the inclusion of the temporal gap) and gave informed consent prior to testing, with all procedures approved by the Ethics Committee of the School of Psychology at the University of Aberdeen.

Procedure

Each participant was tested individually in a single session in a darkened room to minimize infrared reflections and allow for easy detection of peripheral targets. The participant sat (head free) on a height-adjustable chair in front of a bespoke horizontal light emitting diode (LED) grid board. Their index finger was then placed upon the starting location, marked by a tactile Velcro pad on the near side of the board in line with the fixation point. Prior to commencement of each trial, the experimenter gave an auditory "pre-start" cue ("Ready…") and started the trial with an audible key press. The central fixation light appeared (which the participant was required to fixate) for a short duration and was then extinguished, followed by either the immediate appearance of one of the targets ("no gap" condition) or a temporal gap (200 ms for the Studies 1 and 2, 160 ms for Study 3) before the appearance of a target ("gap" condition).

An infrared reflective marker was attached to the index finger of the participant's reaching hand, the position of which was monitored with either a two-camera MacReflex motion analysis system, recording at 60 Hz (Studies 1 and 3) or an Optotrak motion analysis system, recording at 200 Hz (Study 2). The camera positions were calibrated prior to each testing session. Studies 1 and 2 required 200 trials, while Study 3 required 192 trials. Four (Study 1), six (Study 2), and eight (Study 3) different targets were presented.

Results

We report Task (no gap, gap) × hand (right, left) × hemispace (ipsilateral, contralateral) ANOVAs for RT in each study first, and combine all in an omnibus analysis with all 67 participants. Mean RTs as a function of this factor are depicted separately for each study in **Figure 5**.

Study 1

Main effects of Task [$F_{(1, 25)} = 34.16$, $p < 0.001$], Hand [$F_{(1, 25)} = 15.24$, $p < 0.002$] Hemispace [$F_{(1, 25)} = 56.72$, $p < 0.001$] are explained by quicker movement initiation by the left hand (8 ms), in gap trials (22 ms), and in ipsilateral hemispace

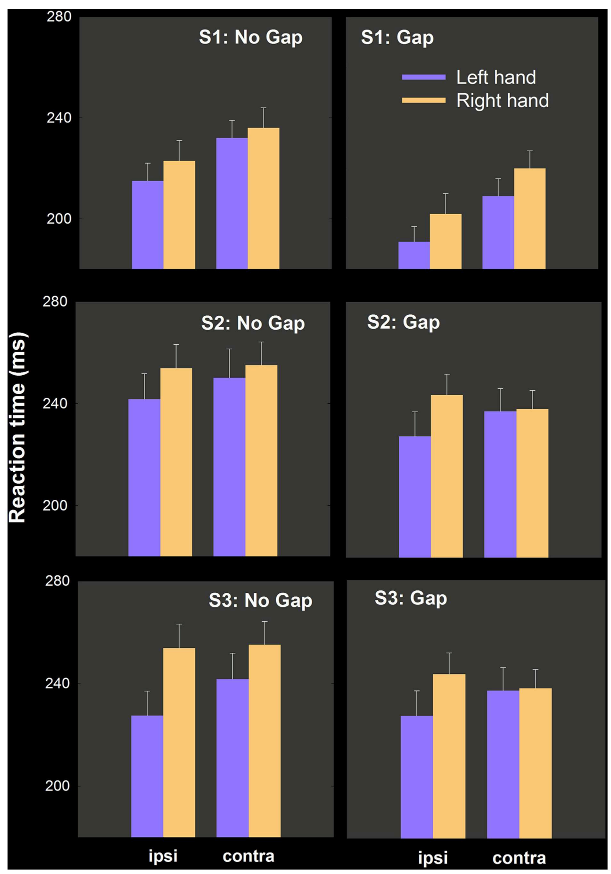

FIGURE 5 | Mean RT as a function of condition (no gap, gap), hand and hemispace. Our prediction was that left hand RT advantages would be enhanced in gap conditions relative to no gap conditions. Significant hand differences in no gap conditions were not modulated statistically by the introduction of a fixation-target gap.

(16 ms). No higher order interactions involving hand and task were obtained, in spite of a numerically larger hand difference in gap (11 ms) vs. no gap (6 ms) conditions in the predicted direction. These means and associated variance estimates are illustrated in the top row of **Figure 5**. As in experiment 1 above, we calculated the proportion of the sample who have numerically smaller left hand RT: in no gap, 18/26 (0.69); in gap, 22/26 (0.85).

Study 2

The same three factor repeated measures ANOVA uncovered significant effects of Task [$F_{(1, 20)} = 8.69$, $p < 0.009$; gap 11 ms quicker than no gap], Hand [$F_{(1, 20)} = 8.09$, $p < 0.02$; left hand quicker by 14 ms] as well as Task by Hand [$F_{(1, 20)} = 9.73$, $p < 0.006$] and Hand by Hemispace [$F_{(1, 20)} = 7.01$, $p < 0.02$] interactions. The three way interaction between Task, Hand, and Hemispace was not significant [$F_{(1, 20)} = 0.14$, N.S.] The relevant means and variance estimates appear in the middle row of **Figure 5**.

The Task by Hand interaction may be due to a significant drop in RT in the right hand [15 ms; $t_{(20)} = 3.26$, $p < 0.005$] but not in the left hand [2 ms; $t_{(20)} = 1.16$, N.S.] in gap relative to no gap conditions (contrary to expectations). The Hand by Hemispace interaction may be due to no significant hemispace effect for the right hand [−1.1. ms; $t_{(20)} = -0.69$, NS] while the left hand was significantly quicker in ipsilateral space [12 ms; $t_{(20)} = 2.91$, $p < 0.01$].

As in experiment 1 and study 1, we calculated the proportion of the sample who have numerically smaller left hand RT in each condition: in no gap, 17/21 (0.81); in gap, 16/21 (0.76).

Study 3

Main effects of Task [$F_{(1, 19)} = 94.12$, $p < 0.001$], Hand [$F_{(1, 19)} = 6.49$, $p < 0.03$], Hemispace [$F_{(1, 25)} = 4.95$, $p < 0.04$] are explained by quicker initiation by the left hand (10 ms), in gap trials (26 ms), and in ipsilateral hemispace (6 ms). As in study 1, no higher order interactions involving hand and task were obtained, in spite of a numerically larger hand difference in gap (14 ms) vs. no gap (8 ms) conditions in the predicted direction. These means and associated variance estimates are illustrated in the bottom row of **Figure 5**. As above, we calculated the proportion of the sample who have numerically smaller left hand RT: in no gap, 13/20; in gap, 13/20 (both = 0.65).

In summary, the RT differences between the hands are small, and for two of three studies 60 Hz recordings have relatively poor temporal resolution, at least on single trials (see General Discussion). We thought that given the completely repeated measures nature of all three studies, we could combine these datasets.

Omnibus analysis

The typical main effects of Task (19 ms; $\eta_p^2 = 0.56$), Hand (11 ms; $\eta_p^2 = 0.28$), and Hemispace (9 ms; $\eta_p^2 = 0.38$) are significant, as in the individual experiments, but of most relevance here are the two way interaction between Task and Hand [$F_{(1, 66)} = 0.007$, NS] and the three way interaction between Task, Hand, and Hemispace [$F_{(1, 66)} = 0.748$, NS]. These data suggest that adding a gap between fixation offset and target onset do not have any effects on the left hand RT advantage.

General Discussion

We report on three sets of studies where we attempted to increase or decrease left hand advantages in RT for visually-guided aiming movements. We used three different tasks to do so: two-target bisecting (linked to right hemispheric specialization), target uncertainty (as a proxy for visuo-spatial processing/localization) and the gap effect (linked to both vigilance and visuospatial orienting, both related to somewhat distinct but nevertheless right hemispheric circuitry). Our results provide very little evidence for any effect of these three manipulations on hand differences in RT.

In experiment 1, we managed to obtain one of those relatively rare aiming samples where left hand RT advantages were not found, which limited the scope for clear attenuation of such effects in bisecting. In experiment 2, quite reliable left hand RT advantages were found in our second sample of right handers, but these were little changed by increasing target number from 6 to 10 or decreasing target number from 6 to 2. In our final experiment, across three separate studies with different participants, there was little suggestion of increased hand differences in RT when comparing gap to no gap conditions. In addition to main effects and the hypothesized two way interaction between hand and task, we looked for evidence if hemispace moderated any differences. It didn't.

Our tasks may not have been optimized for "pushing" a right hemisphere lateralized mechanism for either attentional processes or for visuospatial analysis. In the former case, in all tasks participants waited (vigilantly we hope) for a single target which appeared in a relatively restricted horizontal meridian. Although in bisection two targets needed to be processed, a limited number of such pairs (5), of identical inter-target distances, may have allowed some participants to identify the limited number of response points, or to plan their movements relative to one of the two members of the pair, etc. With current stimulus generation/display capabilities there is no reason why bisection performance could not be required with varying pair sizes and orientations in space, which might tax any visuospatial mechanisms to a greater extent than our relatively simple stimulus display (which was designed for use with elderly participants; Goodale et al., 1990).

We have rather little data, surprisingly, which let us predict what aiming experiments left hand RT advantages are obtained in, vs. those in which they are not. There are suggestions that adding choice to RT experiments may typically elicit right hand advantages, but to our knowledge this type of manipulation hasn't been varied systematically, at least in the hand difference literature. Similarly, the importance of visually-guided reaching for left hand RT advantage has yet to be decisively established, relative to, simple RT in detection tasks, for example. One group claim that the left hand RT advantage in the same participants depends on actually making a reach to a target (Mieschke et al., 2001), while another group claims that it does not (Barthélémy and Boulinguez, 2002). These studies may be limited somewhat by their small number of targets and/or participants. They also approach their data sets quite differently in statistical terms. One of us is currently attempting a replication of these experiments with a larger sample. Our gap effect manipulation was designed as a first pass within this domain, but was unsuccessful.

Given the failure to find a left hand RT advantage in the pointing task of experiment 1, it could be useful to perform power calculations for informing sample size requirement in future tasks. In fact, such an estimate is difficult to calculate, given that hand is a repeated measure in these designs and the variance of the difference scores, as well as the correlation between right and left hand RT, are needed for the calculations (Dunlap et al., 1996; Morris and DeShon, 2002; Maxwell et al., 2008). These measures are not provided in published papers. In addition, we now prefer a point estimate/accuracy approach to sample size planning, as advocated by Kline (2005), Maxwell et al. (2008), and Cumming (2012). These techniques avoid questions of how large an effect size exists in the population. Instead, experimenters consider how large confidence intervals could be before a particular sample would become uninformative.

For these estimates of sample size for precision, we created an estimate of standard deviation of hand RT differences from the current five and an additional eight in-house studies, where variance of the difference scores was known in each. Using the techniques of Cumming (2012) we estimate that a sample size of at least 17 people is required, *on average*, to ensure that a 95% confidence interval surrounding a left hand RT advantage does not overlap with zero. To ensure that 99% of the time the confidence interval would never overlap with zero (what Cummings refers to as the "with assurance" calculation), a sample size of 28 is required (see Supplementary Materials for additional information and a figure depicting estimated CI size and sample size).

We have to acknowledge that the left hand RT advantage may not depend on its' privileged connections to the right hemisphere. In fact, it is equivalently parsimonious to consider the typical difference as *an increase* in right hand RT; it may be related to superior motor control capacity of the left hemisphere in most conventionally dominant dextrals, or may even be related to many years' experience of skilled sensorimotor activity related to drawing and writing with the preferred hand. Of course such experience might manifest itself in specialized networks of the left hemisphere, but these may depend on practice and experience. In any case, the suggestion that the hand difference is not related to innate processing pre-dispositions of the left or right cerebral hemisphere, is a testable one: quantify the same dependent measures in left-handed participants. Although most left handed people, like their right handed counterparts, are left hemisphere dominant for speech and language, the proportion is smaller in this group (roughly 70 vs. 95% in right handers; Rasmussen and Milner, 1977). If directional behavioral results (e.g., hand differences, ear advantages in dichotic listening, or visual field biases) depend on hemispheric asymmetry, they will mimic the direction of difference in dextrals (left hand RT < right hand RT; right ear syllable score greater than left ear syllable score, etc.). The magnitude of the effect, however, will be reduced. This reduction would follow a small proportion of the adextral group having bilateral or reversed cerebral dominance (Carey and Johnstone, 2014)[2].

We hesitate at this stage to avoid the ubiquitous but often trite suggestion that "further research is needed." The more interesting question is what kind of research is needed (or if any indeed is required—this effect, when obtained is quite small; approximately 7 ms on average, based on 13 separate hand difference studies in our laboratory.

First, we would suggest that any sort of speed-accuracy trade off in the left hand relative to the right be systematically eliminated as a major factor in left hand RT advantages (such a suggestion has been made in the reciprocal tapping literature, for example; see Carson, 1992, for review). We already know that if there is such a trade-off, it would have to do with pre-movement processing, as the dominant hand of the right hander is faster and more accurate, once it is off the mark. Our accuracy data of experiment 1 (see Supplementary Materials) suggest that this is unlikely, but perhaps this hypothesis needs to be eliminated more systematically, within subject, on a trial by trial basis. In fact, in hand-visible reaching, accuracy differences tend to be quite small, and are often restricted to increased variability in the left hand of the right hander (e.g., Roy and Elliott, 1989; Carson et al., 1990). Often we don't bother to measure it, and restrict our analysis instead to speed-related dependent measures. In any case, we certainly see little evidence for speed accuracy trade-offs across participants, in experiment 1 or in other experiments we have performed.

Another approach to addressing mechanisms accounting for left hand RT advantages might consider the distributions of left and right handed movement RTs in participants who show these effects robustly, and then characterize them in much more detail than the usual mean/ANOVA approach that many scientists in this domain have favored. For example, are the distributions shifted by approximately 8–10 ms, or is there a small population of very fast left-handed movements, roughly analogous to "express saccades" seem in the saccadic gap literature (e.g., Wenban-Smith and Findlay, 1991)?

Carson (1996) has suggested that the spatial demands of reaching may be relatively impervious to these types of manipulations of the stimulus, suggested by several experiments by him and his colleagues which fail to affect the left hand RT advantage (as well as the three experiments reported here). His later comments on left RT advantages introduced the idea of "spatial parametrization," integrating information about parts of the body in a feedforward manner for comparison to elements of the environment (Carson et al., 1995; Carson, 1996). The idea seems similar to the literature on the coordinate transformations required to get from a retinal representation of target position to a hand- or arm-centered scheme (reviewed in Carey, 2004;

[2]Remarkably little is known, in adextrals, about asymmetries that tend to favor the right hemisphere in dextrals, beyond face processing (although see Elias and Bryden, 1998. A second paper on prosody has a promising title suggesting a comparison of left and right handers. Sadly it has a sample size of two in each group: Perry et al., 2001).

Crawford et al., 2011). More details on this sort of idea are probably necessary to generate testable hypotheses for reaching experiments. The literature on coordinate transformations has grown considerably since the 1990s, but it is not obvious to us how some of these computations would map neatly onto ideas about the right hemisphere. In fact, different scientists have argued, based on quite distinct sensorimotor tasks, that feedforward (e.g., Meyer et al., 1988; Adam et al., 2010) or feedback processes (e.g., Roy et al., 1994) favor left hemisphere-right hand sensorimotor control.

The "face validity" of linking left hand RT advantages to some sort of right hemispheric process still has some appeal. If these hand differences (RT, accuracy, peak velocity, duration) are related to relatively innate cerebral specializations, then predictions can be made about the same dependent measures when assessed in visually-guided reaching movements of left handers. In other words, if these effects are strongly related to cerebral asymmetries, then many left handers (roughly 70% are left hemisphere dominant for speech and language) should behave like right handers, literally (left hand RT advantages, right hand duration and peak velocity advantages, etc.). There is some evidence for this state of affairs (Boulinguez et al., 2001a,b) or at least for weakened (but not reversed) asymmetries in a group of left handers (Goodale, 1990). The discrepancies may be partially resolved by a more detailed description of both the depth and breadth of hand preferences in both right and left handers, as well as consideration of the proportions of individuals in each group which show any directional effect (Carey and Johnstone, 2014).

Acknowledgments

We are grateful to Lorna Jakobson, A. David Milner, Irene Logan, John Orphan, Phil Surette, and Jim Urqhuart for expert technical assistance. Leah T. Johnstone and two anonymous referees provided detailed comments on this manuscript. This research was supported by Medical Research Council of Canada Grant MA-7269 to MG and a Wellcome Trust Travel Grant to DC.

Supplementary Material

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2015.01203

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