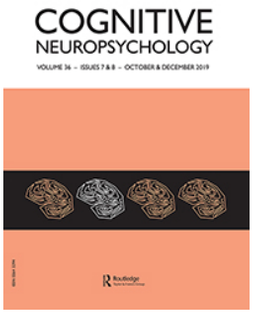
Routledge
Taylor & Francis Group



Cognitive Neuropsychology

ISSN: 0264-3294 (Print) 1464-0627 (Online) Journal homepage: www.tandfonline.com/journals/pcgn20

Bimanual visually guided movements are more than the sum of their parts: Evidence from optic ataxia

Celia Litovsky, Feitong Yang, Jonathan Flombaum & Michael McCloskey

To cite this article: Celia Litovsky, Feitong Yang, Jonathan Flombaum & Michael McCloskey (2019) Bimanual visually guided movements are more than the sum of their parts: Evidence from optic ataxia, Cognitive Neuropsychology, 36:7-8, 410-420, DOI: 10.1080/02643294.2020.1724922

To link to this article: https://doi.org/10.1080/02643294.2020.1724922

Published online: 13 Feb 2020.

Submit your article to this journal

Article views: 169

View related articles

View Crossmark data

Citing articles: 1 View citing articles

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=pcgn20

COGNITIVE NEUROPSYCHOLOGY
2019, VOL. 36, NOS. 7–8, 410–420
https://doi.org/10.1080/02643294.2020.1724922

Routledge
Taylor & Francis Group

REPORT

Check for updates

Bimanual visually guided movements are more than the sum of their parts: Evidence from optic ataxia

Celia Litovsky[a], Feitong Yang[b], Jonathan Flombaum[b] and Michael McCloskey[a]

[a]Department of Cognitive Science, Johns Hopkins University, Baltimore, MD, USA; [b]Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, USA

ABSTRACT

Many reaching actions involve both hands. An open question is whether two-handed reaching involves two simultaneous, independent unimanual reaches, or recruits additional or different processes than those mediating one-handed reaching. We tested optic ataxic patient MDK on a set of unimanual and bimanual reaching tasks. Although MDK was impaired in both types of reaching task, his bimanual reaching was considerably better than his unimanual reaching. These results imply that bimanual reaching involves different or additional processes relative to unimanual reaching. We suggest that bimanual reaching may involve monitoring of the distance between the two hands relative to the distance between the two targets.

ARTICLE HISTORY
Received 6 September 2019
Revised 29 December 2019
Accepted 28 January 2020

KEYWORDS
Bimanual reaching; unimanual reaching; optic ataxia

Introduction

Many reaching actions involve coordinated movements of both arms (e.g., picking up a large box). However, research on cognitive and neural mechanisms in reaching has focused largely on unimanual reaching (for a review, see Lacquaniti & Caminiti, 1998), with fewer studies examining bimanual reaching (see Witney, 2004, for a review of research on bimanual motor performance). One important unresolved question is whether bimanual reaching is best conceptualized as involving two simultaneous but independent unimanual reaches, or whether instead bimanual reaching recruits processes different from, or in addition to, those underlying unimanual reaching (e.g., processes that coordinate the movements of the two limbs).

Diedrichsen, Nambisan, Kennerley, and Ivry (2004) asked neurotypical participants to reach unimanually to a visual target, or bimanually to two separate targets. On some trials targets were displaced during the reaching movements. Diedrichsen et al. found that adjustments of arm trajectories in response to target displacement were as efficient in bimanual as in unimanual reaching, and concluded that the two limbs operated independently during bimanual movements. Similarly, Tresilian and Stelmach (1997) found that maximum grip apertures and response times were comparable for unimanual and bimanual reach-to-grasp tasks. In contrast, other researchers have reported evidence suggesting that relative to unimanual reaching, bimanual reaching implicates different or additional processes (e.g., Asai, Sugimori, & Tanno, 2010; Kelso, Southard, & Goodman, 1979). For example, in the Kelso et al. (1979) study participants reached to large, close targets (easy targets) and to small, distant targets (difficult targets). For unimanual reaching, and for bimanual reaching with both targets of equal difficulty, reaches were performed more quickly for easy than for difficult targets. However, in bimanual conditions with one easy and one difficult target, reaches to the easy target were slowed, such that both hands reached their targets simultaneously, or nearly so. This result suggests some form of coordination between limbs in bimanual reaching.

In the present study we explored unimanual and bimanual reaching in an individual (MDK) with impaired visually-guided reaching (optic ataxia) resulting from a neurodegenerative disease. As with reaching research in general, studies of optic ataxia have focused on unimanual reaching (e.g., Goodale et al., 1994; Milner & Goodale, 1998; Vindras et al., 2016), and we are aware of only one study that reports results from bimanual reaching tasks. Perenin and

CONTACT Celia Litovsky litovsky@jhu.edu 3400 N. Charles St., Krieger Hall, Room 237, Baltimore, MD 21218, USA
© 2020 Informa UK Limited, trading as Taylor & Francis Group

Vighetto (1988) compared unimanual and bimanual reaching performance in 10 optic ataxic patients, and found that most patients showed greater impairment in the bimanual task. This result might reflect differences in the processes underlying unimanual and bimanual reaching. Another possibility, however, is that unimanual and bimanual reaching recruit the same processes, with the poorer bimanual reaching performance reflecting simply the increased cognitive load (e.g., higher working memory demand) involved in reaching simultaneously to two spatial locations (e.g., Spiegel, Koester, & Schack, 2013).

We tested MDK's unimanual and bimanual reaching, and found a pattern of results that was both novel and informative. Although MDK was impaired in both unimanual and bimanual reaching tasks, his bimanual reaching performance was in most respects significantly better than his performance in unimanual reaching. This pattern cannot be explained in terms of cognitive load, and strongly suggests differences in the processes underlying unimanual and bimanual reaching.

We first present a brief case history, and demonstrate that MDK shows the typical optic ataxia pattern in unimanual reaching: accurate reaching to fixated targets (Experiment 1) but grossly impaired reaching to peripheral targets (Experiment 2). We then compare MDK's unimanual and bimanual reaching (Experiment 3), and discuss the implications of our findings.

Case report

MDK is a 71-year-old right-handed male with a PhD in Physics and Astronomy. Three years prior to testing, he was diagnosed with posterior cortical atrophy (PCA), and a structural MRI obtained during the study shows mild bilateral posterior parietal and occipital cortical atrophy (see Figure 1). In-house perimetry testing revealed no visual field defects. MDK showed no primary motor deficits at clinical assessment, nor did he show any evidence of apraxia.

Experiment 1: Reaching to fixated targets

Experiment 1A: Reaching to fixated dots

MDK sat 40 cm from a computer monitor with his head resting in a chin rest. On each trial he fixated a white cross in the centre of a blank gray screen, and indicated when he was ready. A 1°-diameter white target dot was then presented at one of 24 possible locations and remained on the screen throughout the trial (see Figure 2A for an example). MDK shifted his gaze to

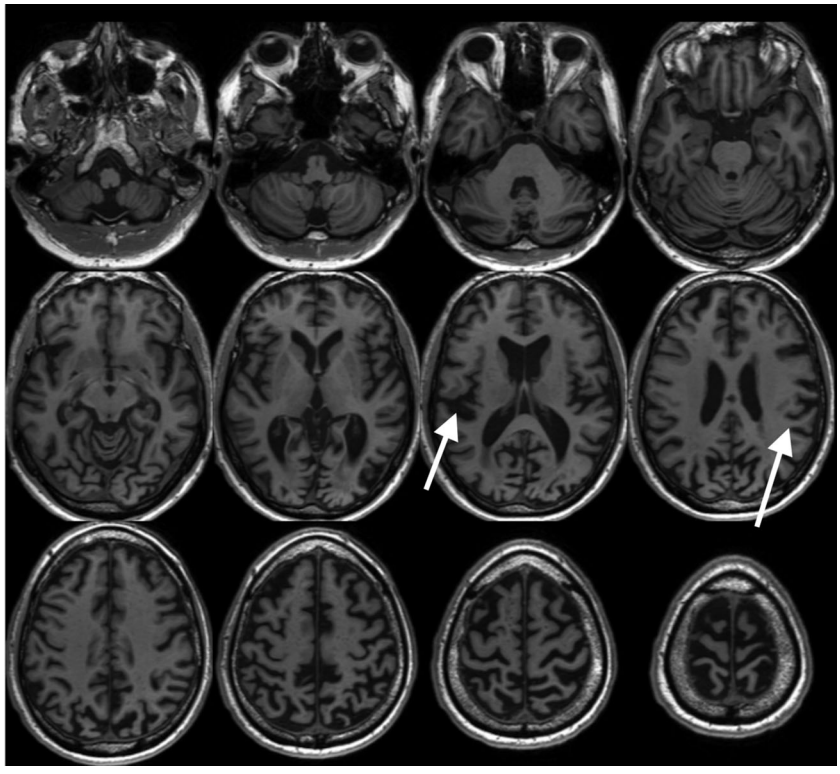


Figure 1. Structural MR images obtained during the study. Arrows indicate areas of cortical atrophy.

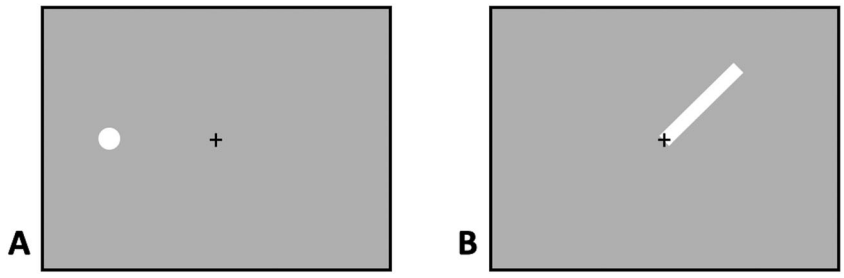


Figure 2. A. Example of dot stimulus from Experiment 1A. B. Example of bar stimulus from Experiment 1B.

the target and then reached to it with his right or left index finger. MDK kept his finger on the screen until the experimenter recorded his response with a mouse-click at the finger position. Target locations included eight angular directions from fixation (0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°) at three eccentricities (6, 12, and 18 degrees of visual angle). Data for left- and right-hand reaching were collected in separate blocks, with 48 trials for each hand.

Experiment 1B: Reaching to fixated ends of bars

On each trial a red bar was presented, extending from fixation at one of 8 orientations (0°, 45°, 90°, 135°, 180°, 225°, 270°, or 315°; see Figure 2B for an example). The bar was 0.7° wide and 6°, 12°, or 18° long. At the start of each trial, MDK fixated a central cross. When the stimulus was presented, he shifted his gaze to the peripheral end of the bar, and then reached to that end with his left or right hand. Procedures were otherwise the same as in Experiment 1A.

Results

As illustrated in Figures 3 and 4, MDK reached accurately to fixated targets. To assess accuracy quantitatively, we represented target and response locations in polar coordinates (distance and angular direction from the central cross MDK fixated at the start of a trial). Distance accuracy was assessed via the ratio DR/DT, where DR and DT are the distances of the response and target locations, respectively, from the central cross. A ratio of 1 indicates a correct reaching distance, with ratios less or greater than 1 indicating under- and over-shooting of the target, respectively. MDK's reaching distances to fixated dots and bars were highly accurate: his mean distance ratios were 1.01 with each hand for dots, and 1.00 with each hand for bars.

We assessed directional accuracy by calculating the absolute angular difference between target and response locations. MDK's mean angular error was minimal for both dots (2.52° for the right hand, and 3.04° for the left) and bars (1.27° and 2.54° for right and left hands, respectively).

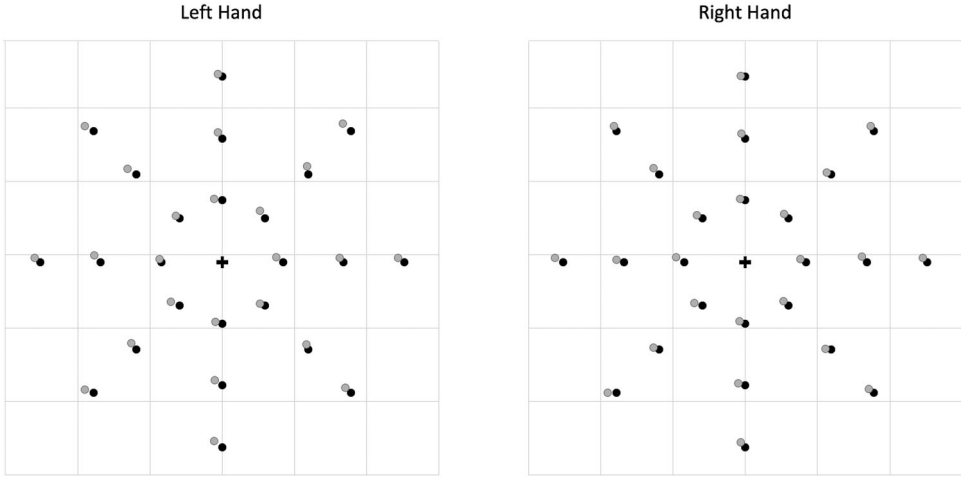


Figure 3. MDK's reaching responses to fixated dots. Black dots are target locations, and gray dots show the mean reaching location for each target.

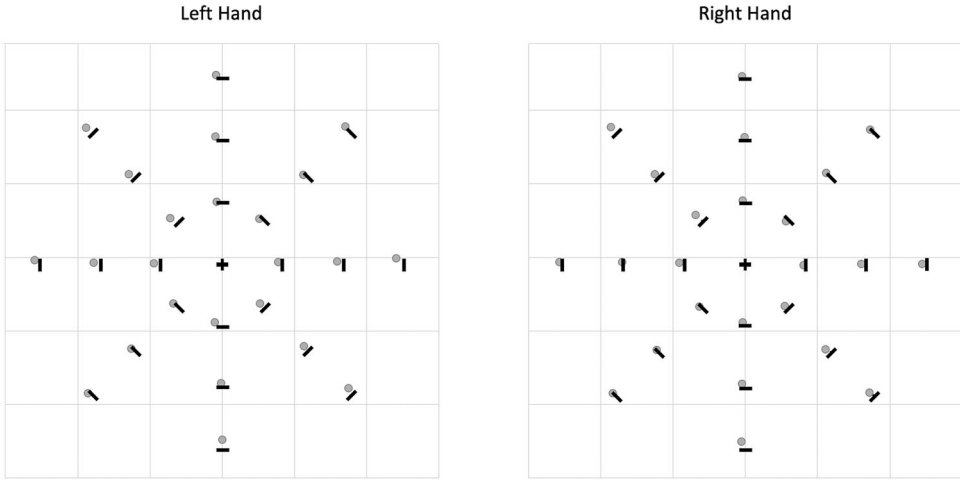


Figure 4. MDK's reaching responses to fixated bar ends. Black dashes represent target locations (far ends of bars), and gray dots show the mean reaching location to each target.

Experiment 2: Reaching to peripheral targets

Experiment 2A: Reaching to peripheral dots

On each trial a 1° target dot was presented for 200 ms at one of 24 locations (the same target locations as in Experiment 1). MDK was instructed to maintain fixation on the central cross throughout the trial, and fixation was monitored with an EyeLink eye tracker (SR Research; sampling rate 500 Hz). Upon stimulus offset, MDK reached to the target location with his right or left index finger, while maintaining central fixation. Right- and left-hand reaching were tested in separate trial blocks, with a total of 264 and 192 trials for right and left hands, respectively. Twelve trials (10 right-hand and 2 left-hand) were excluded from analyses because MDK stated that he did not see the target or because he failed to maintain fixation.

Experiment 2B: Reaching to peripheral ends of bars

In this experiment target bars identical to those in Experiment 1B were presented for 200 ms, and MDK reached to the distal end of the bar while maintaining central fixation. For each hand 102 trials were collected. Fourteen trials (6 left-hand and 8 right-hand) were excluded from analyses due to experimenter error or MDK's failure to maintain fixation.

Results

MDK grossly undershot the target locations when reaching to peripheral stimuli, as shown in Figures 5 and 6. For dots his mean distance ratios were .35 for right-hand reaching and .42 for left-hand reaching, and for bars the ratios were .45 (right hand) and .48 (left hand). Mean distance ratios were slightly higher for bars than for dots, indicating slightly less undershooting of the target, $F(1,340) = 29.06$, $p < .001$ (right hand) and $F(1,282) = 8.95$, $p < .01$ (left hand). For both dots and bars, however, MDK reached on average less than half the actual distance to the target. All of the distance ratios for peripheral stimuli were reliably lower than the corresponding ratios for fixated stimuli (1.01 for dots and 1.00 for bars), Fs > 300, ps < .0001.

In some reported cases of optic ataxia, impaired reaching to peripheral targets is largely restricted to one hand, one visual hemifield, or both (Binkofski & Fink, 2005; Blangero et al., 2008; Perenin & Vighetto, 1988; Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006). For MDK the undershooting of peripheral targets was observed for both left- and right-hand reaching to both the left and right visual hemifields, although some effects of hand and visual field were observed. The deficit was more severe for left visual field (LVF) than right visual field (RVF) targets, $F(1,331) = 15.06$, $p < .001$ for dots, and $F(1,138) = 15.39$, $p < .001$, for bars. For dots, the left hand reached more accurately than the right hand, $F(1,331) = 15.43$, $p < .001$, but no significant difference was found between left- and right-hand reaching for bars ($F < 1$). A hand by visual field interaction was observed for both bars, $F(1,138) = 29.20$, $p < .001$, and dots, $F(1,331) = 21.70$, $p < .001$, indicating that the right hand reached more accurately in the RVF than in the LVF, but the left hand

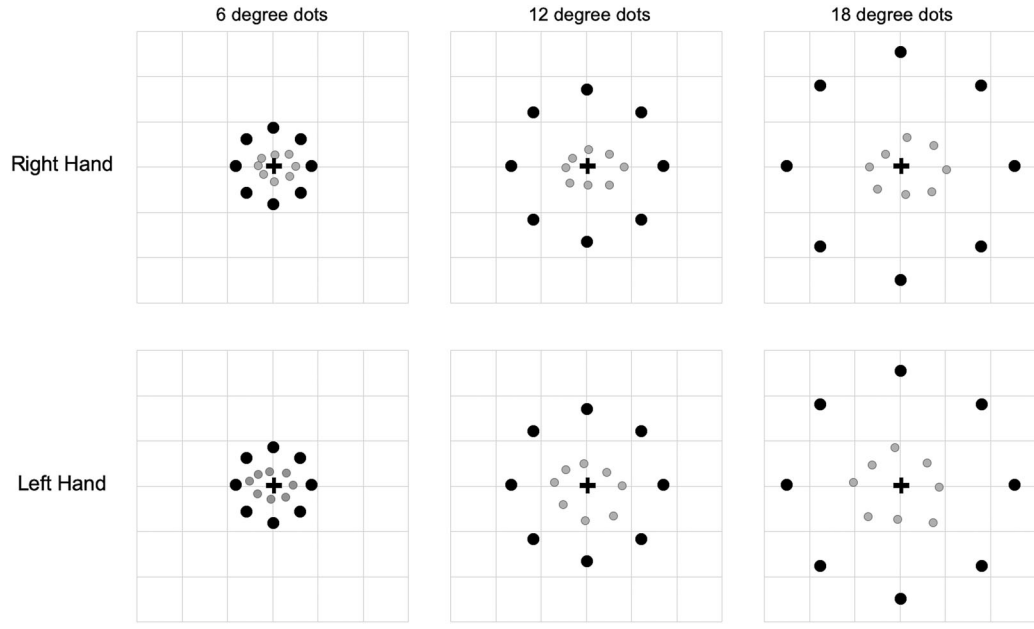


Figure 5. MDK's reaching responses to peripheral dots. Black dots represent target locations, and gray dots show the mean reaching location to each target.

shows no difference in accuracy in reaching to either visual field.

MDK's pattern of accurate reaching for fixated targets and undershooting for peripheral targets is typical among reported cases of optic ataxia (e.g., Blangero et al., 2010; Khan et al., 2005), although overshooting of targets in the near periphery and undershooting of targets in the far periphery has occasionally also been observed (Perenin & Vighetto, 1988; Ratcliff & Davies-Jones, 1972).

MDK's directional accuracy for peripheral targets was reasonably good, although not quite as good as for fixated targets. Mean angular errors for peripheral dots were 9.42° (right hand) and 10.17° (left hand).

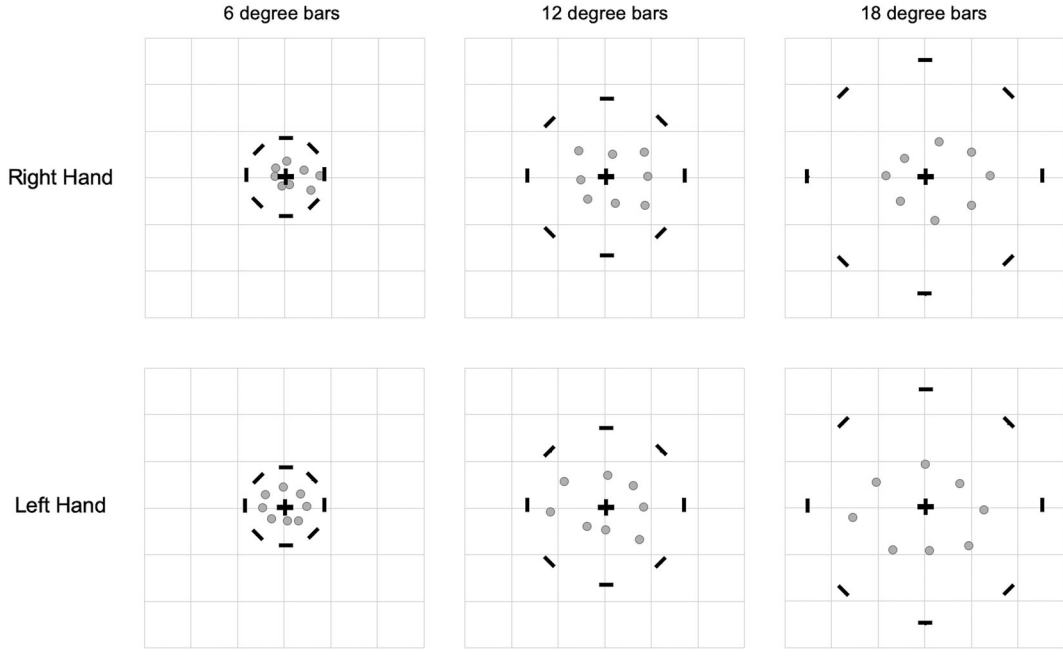


Figure 6. MDK's reaching to peripheral bar ends. Black dashes represent target locations (peripheral ends of bars), and gray dots show the mean reaching location to each target.

Mean angular errors for peripheral bars were 13.27° (right hand) and 7.20° (left hand).

Experiment 3: Unimanual versus bimanual reaching

Experiment 3A: Dots

This experiment compared unimanual and bimanual reaching to dots. In the unimanual condition MDK reached with one hand to one of two target dots, whereas in the bimanual condition he reached to both dots, one with each hand.

MDK fixated a central cross while two dots were presented for 200 ms. One dot was positioned at the central fixation point, and the other was 7.5°, 15°, or 30° to the left or right of fixation. The dots were aligned horizontally on all trials because MDK expressed uncertainty about how to reach bimanually to vertical and diagonal dot configurations.

In the unimanual condition, MDK was instructed to reach to either the right or left dot with his right or left index finger, respectively, while maintaining central fixation. Right- and left-hand reaching were tested in different blocks. Reaching to peripheral and fixated targets was tested in separate blocks. Peripheral dots were always in the hemifield ipsilateral to the reaching hand (e.g., the left hand reached to LVF targets, and the right hand reached to RVF targets). In the bimanual condition, MDK was instructed to reach to both dots while maintaining central fixation. On all bimanual trials, he reached to the leftmost dot with his left hand, and to the rightmost dot with his right hand. Under this procedure, stimuli and response hands were matched between unimanual and bimanual conditions.

Over three sessions, 90 trials were collected for each hand in the unimanual condition, and 90 trials were collected in the bimanual condition. Five trials in each condition were excluded when MDK indicated that he did not see one of the targets or because he failed to maintain fixation, resulting in a total of 175 unimanual and 85 bimanual trials.

Experiment 3B: Bars

Stimuli in this experiment were horizontal bars 0.7° wide and 7.5°, 15°, or 30° long, presented for 200 ms. For all target bars, one end was anchored at the central fixation point, and the other end was to the left or right of fixation (see Figure 7 for examples).

In the unimanual condition, MDK reached to either the right or left end of the target bar with his right or left index finger, respectively, while maintaining central fixation. Reaching to peripheral and fixated targets was tested in separate blocks. Peripheral bar ends were always in the hemifield ipsilateral to the reaching hand (e.g., the left hand reached to LVF

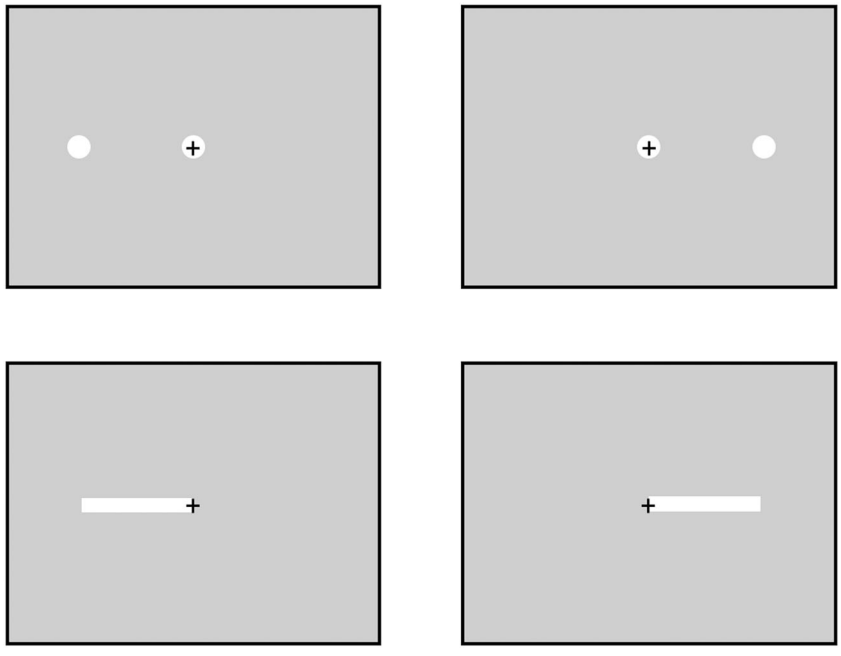


Figure 7. Examples of dot and bar stimuli from Experiment 3.

targets, and the right hand reached to RVF targets). In the bimanual condition, MDK reached to both ends of the target bar while maintaining central fixation. On all bimanual trials, he reached to the left end of the bar with his left hand, and to the right end with his right hand. Over three sessions, 81 trials were collected for each hand in the unimanual condition, and 60 trials were collected in the bimanual condition. Ten unimanual trials were excluded (4 right-hand and 6 left-hand trials) when MDK indicated that he did not see the target, for a total of 152 unimanual trials.

Results

Results for dot and bar stimuli are presented in Figure 8 and Figure 10, respectively. Dark gray dots show MDK's mean response locations for unimanual reaching, and light gray dots show mean bimanual reaching locations.

Considering first the dot stimuli (Experiment 3A), the unimanual condition showed the same pattern observed in the previous experiments: Accurate reaching to fixated targets (here, the dots coinciding with the fixation point), and undershooting of peripheral targets.

In bimanual reaching MDK's performance was somewhat different, and in fact better. He reached accurately to fixated (central) dots and to the least eccentric peripheral dots (7.5°). MDK undershot the more eccentric peripheral dots (15° and 30°), but to a lesser extent than in unimanual reaching. Peripheral response locations were significantly farther from fixation in bimanual than in unimanual reaching, $F(1, 81) = 52.32$, $p < .0001$ (left hand, LVF stimuli); $F(1, 81) = 47.64$, $p < .0001$ (right hand, RVF stimuli). Mean peripheral response locations were 3.9° (LVF stimuli) and 3.4° (RVF stimuli) farther from fixation in bimanual than in unimanual reaching. Mean central response locations were not significantly different for bimanual versus unimanual reaching.

The differences between unimanual and bimanual conditions may also be described in terms of the distance between the response locations for the two hands. Figure 9 plots the distance between the mean central and peripheral response locations for unimanual and bimanual reaching. As is evident in the figure, these response distances were consistently larger—and consistently closer to the correct distances—for bimanual than for unimanual reaching, $F(1, 168) = 56.44$, $p < .0001$.

For the bar stimuli (Experiment 3B), differences between MDK's unimanual and bimanual reaching were even greater. In unimanual reaching he was again accurate for the central bar ends, and undershot the peripheral bar ends (except for the shortest LVF bars). In the bimanual condition MDK reached accurately to the fixated bar end for LVF stimuli, but for

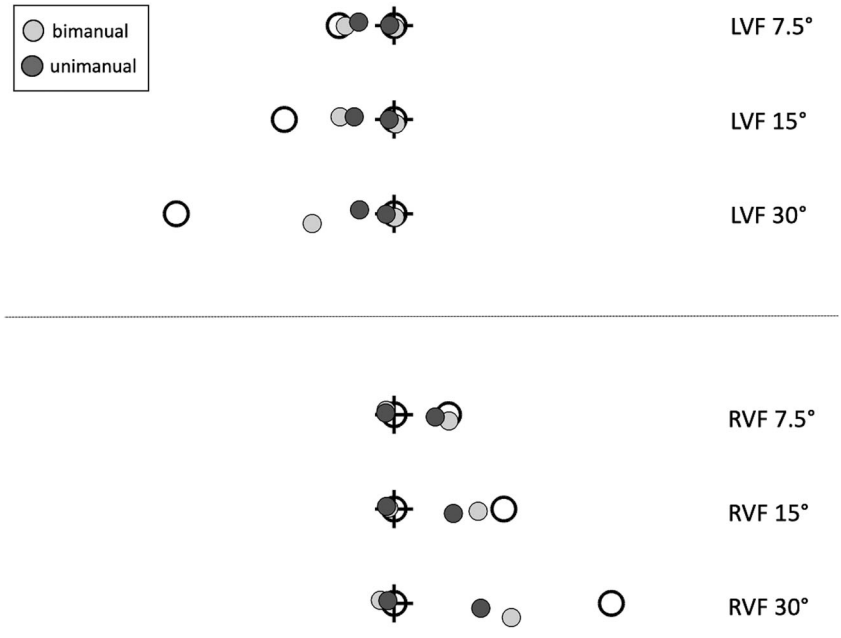


Figure 8. MDK's unimanual and bimanual reaching performance to two dots. Unfilled dots are target locations, dark gray dots show unimanual mean reaching locations, and light gray dots show bimanual mean reaching locations.

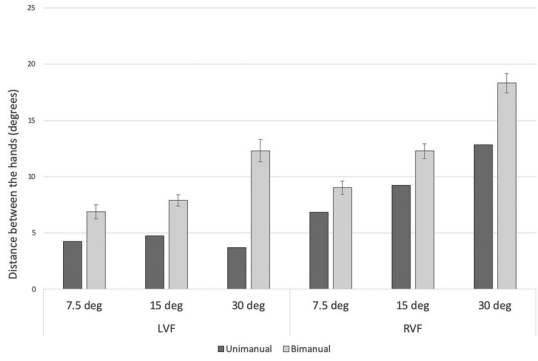


Figure 9. MDK's mean distance between hands for tasks with dots stimuli. Bimanual error bars represent the standard error of the mean.

RVF stimuli his reaches to the fixated bar ends were displaced somewhat leftward. Most notably, however, MDK showed much less undershooting of peripheral target locations in bimanual than in unimanual reaching. In fact his bimanual reaching showed overshooting of peripheral bar ends for the two shortest LVF stimuli (see Figure 10).

MDK's peripheral response locations were significantly farther from fixation for bimanual than for unimanual reaching, $F(1, 72) = 136.66$, $p < .0001$ (left hand, LVF stimuli); $F(1, 73) = 85.86$, $p < .0001$ (right hand, RVF stimuli). Mean peripheral response locations were 7.7° (LVF stimuli) and 4.4° (RVF stimuli) farther from fixation in bimanual than in unimanual reaching. Mean central response locations were not significantly different for bimanual versus unimanual reaching in the LVF. In RVF trials, MDK's left (central) hand shifted leftward for bimanual reaching relative to unimanual reaching.

Figure 11 plots the distance between the mean central and peripheral response locations for unimanual and bimanual reaching. The response distances were consistently larger for bimanual than for unimanual reaching, $F(1, 151) = 295.2$, $p < .0001$.

To assess whether MDK's better bimanual than unimanual reaching might be attributable to a speed-accuracy tradeoff, we examined reaction times. We ran an additional 96 bimanual trials and 192 unimanual trials each for dots and bars and video-recorded MDK's reaching. Reaction time on each trial was measured as the interval between target offset and the moment MDK's hand touched the screen. For bimanual trials the reaction time for the hand reaching to each target was scored, for comparison with reaches to these same locations in the unimanual condition. We observed the usual pattern of more accurate bimanual than unimanual reaching, and reaction time did not differ between unimanual ($M = 991$ ms) and bimanual trials ($M = 1005$ ms), $F(1, 726) = 1.10$, $p > .1$. These results argue strongly against a speed-accuracy tradeoff as an explanation for the difference between MDK's unimanual and bimanual reaching accuracy.

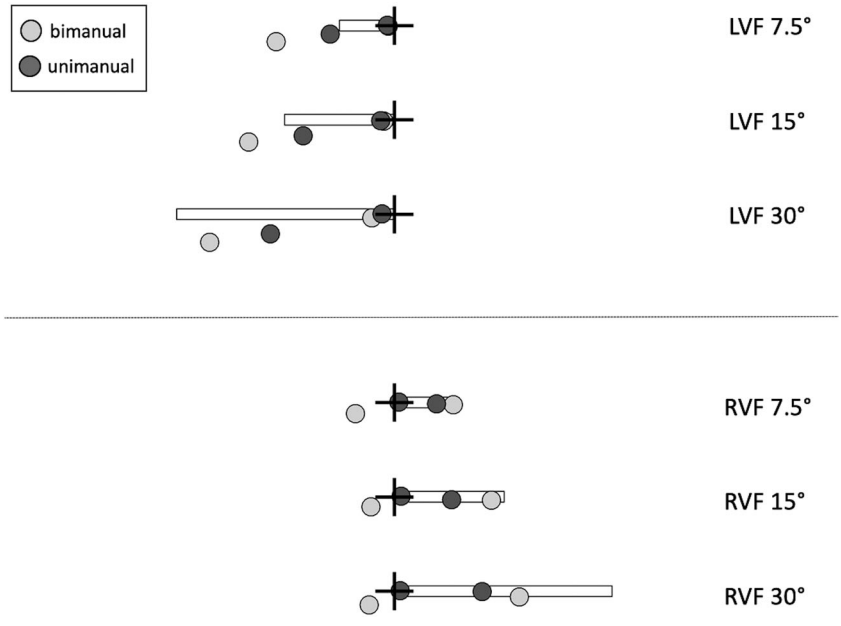


Figure 10. MDK's unimanual and bimanual reaching performance to peripheral bars. Dark gray dots show unimanual mean reaching locations; light gray dots show bimanual mean reaching locations.

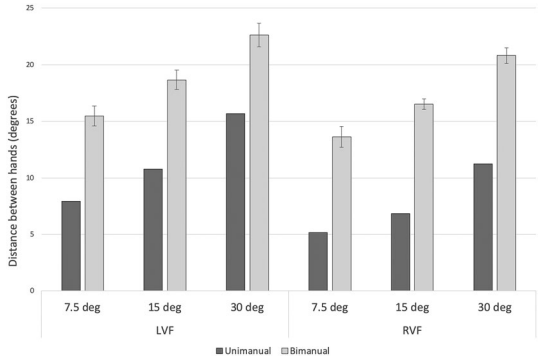


Figure 11. MDK's mean distance between hands for tasks with bar stimuli.

Our results point to some difference(s) in the processes underlying unimanual and bimanual reaching. One possibility is that bimanual reaching is mediated by visuomotor processes that are separate, at least at some level(s), from the processes underlying unimanual reaching. On this account, MDK's unimanual and bimanual reaching processes are both impaired, but the impairment to the bimanual processes is milder. A second possibility is that unimanual and bimanual reaching share underlying processes, but bimanual reaching recruits additional processes as well. For example, bimanual reaching may implicate not only processes that direct the two hands individually to their separate targets, but also processes that monitor and adjust the distance between the reaching hands in an effort to match the distance between the targets.

To determine if bimanual reaching utilizes a process that adjusts the two hands' positions, we probed MDK's hand positions on each bimanual reaching trial. For each trial in the bimanual conditions, we computed the horizontal displacement of each hand's response location from the mean response location for that condition. For example, in the condition with dots at fixation (0°) and 15° to the right of fixation (+15°), the mean response locations were −0.7° and + 11.5°, respectively. On a trial where MDK reached to −1° and + 12°, the displacements were coded as −0.3° and + 0.5°, respectively. If the two reaches on a bimanual trial are independent, we would expect the displacements for the two hands to be uncorrelated. For example, on a trial in which the right hand reached farther to the right than usual for that condition, the left hand might reach farther than average to the left or farther than average to the right. In contrast, if the distance between hands were being monitored in an effort to match the target distance, we might expect the horizontal displacements to be correlated across hands—for example, if the right hand reached farther than usual to the right, the left hand might also reach farther than usual to the right.

We computed the correlation between hands for bimanual dots conditions and (separately) for bimanual bars conditions. For both dots and bars we obtained a significant positive correlation of .30 (dots: $r(83) = .30$, $p < .01$; bars: $r(58) = .30$, $p < .05$), indicating that on bimanual trials the response location for one hand carried information about the response location for the other hand. To confirm that the correlation expected in the absence of coordination between hands was 0 under the rather complicated circumstances of the analyses (targets at varying distances and directions from fixation), we conducted Monte Carlo simulations. On each of 100,000 iterations, we randomly re-paired the the right- and left-hand responses within each eccentricity × visual field condition (e.g., the right-hand response from one trial with the left-hand response for a different trial), and computed the correlation between left- and right-hand displacements. As expected, the mean correlations were near-zero (−.0002 for dots and −.0003 for bars), and significantly lower than the actual correlations of .30 ($ps \leq .01$).

Discussion

We have reported a novel finding with implications for understanding the processes underlying unimanual and bimanual reaching. MDK showed impairment in both unimanual and bimanual reaching tasks, but in most respects his performance was better in bimanual reaching—that is, he performed better when reaching simultaneously for two visual targets than when reaching to a single target. Relative to unimanual tasks, his reaches in bimanual tasks usually landed closer to the targets, and the distance between his response locations for the two targets was usually closer to the correct distance. We note, however, that these experiments used one very specific bimanual condition, in which one hand consistently reached for a fixated target and the other reached for a peripheral target; it is possible that alternative displays would have produced different results.

The observed differences between unimanual and bimanual reaching performance argue against the view that bimanual reaching is accomplished by

simultaneous execution of two independent unimanual reaching processes. Nor can we save a two-unimanual-reaches hypothesis by invoking assumptions about increased cognitive load in bimanual tasks; on this account performance should be worse in bimanual than unimanual reaching, as shown by most of the patients described by Perenin and Vighetto (1988). We might also consider the opposite possibility that cognitive demands are greater for unimanual than bimanual reaching, leading to poorer performance in unimanual conditions. Perhaps, for example, the need to keep track of which stimulus is the target (the fixation point or the peripheral stimulus) adds to the cognitive load in the unimanual condition. However, contrary to what we might expect on this interpretation, MDK's reaction times were not slower in unimanual than bimanual reaching. We also note that most participants in Perenin and Vighetto's (1988) study showed better performance in unimanual than in bimanual reaching, again contrary to what we would expect if unimanual reaching were more cognitively demanding.

We conclude that the processes underlying bimanual reaching differ in some way(s) from those for unimanual reaching. Bimanual and unimanual reaching may implicate quite distinct sets of processes; alternatively, bimanual reaching may recruit not only the processes mediating unimanual reaching, but also employ additional processes. In particular, our finding that errors for the left and right hands were correlated in bimanual reaching suggests a process that monitors and adjusts the distance between hands relative to the distance between targets in bimanual reaching. Our results do not provide definitive evidence for this interpretation, but certainly suggest that it is worth investigating in subsequent research.

Acknowledgements

The authors thank MDK for his participation in our research.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was funded by a Johns Hopkins University Science of Learning Institute grant to Michael McCloskey and a National Science Foundation Graduate Research Fellowship under grant number DGE-1746891 to Celia Litovsky.

References

Asai, T., Sugimori, E., & Tanno, Y. (2010). Two agents in the brain: Motor control of unimanual and bimanual reaching movements. *PLoS One*, *5*(4), e10086. doi:10.1371/journal.pone.0010086

Binkofski, F., & Fink, G. (2005). Apraxien. *Der Nervenarzt*, *76*(4), 493–512. doi:10.1007/s00115-005-1908-7

Blangero, A., Gaveau, V., Luaute, J., Rode, G., Salemme, R., Guinard, M., … Pisella, L. (2008). A hand and a field effect in on-line motor control in unilateral optic ataxia. *Cortex*, *44*, 560–568. doi:10.1016/j.cortex.2007.09.004

Blangero, A., Ota, H., Rossetti, Y., Fujii, T., Ohtake, H., Tabuchi, M., … Pisella, L. (2010). Systematic retinotopic reaching error vectors in unilateral optic ataxia. *Cortex*, *46*(1), 77–93. doi:10.1016/j.cortex.2009.02.015

Diedrichsen, J., Nambisan, R., Kennerley, S. W., & Ivry, R. B. (2004). Independent on-line control of the two hands during bimanual reaching. *European Journal of Neuroscience*, *19*, 1643–1652. doi:10.1111/j.1460-9568.2004.03242.x

Goodale, M. A., Meenan, J. P., Bulthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, *4*, 604–610. doi:10.1016/s0960-9822(00)00132-9

Kelso, J. A. S., Southard, D. L., & Goodman, D. (1979). On the coordination of two-handed movements. *Journal of Experimental Psychology: Human Perception and Performance*, *5*(2), 229–238. doi:10.1037/0096-1523.5.2.229

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., … Rossetti, Y. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience*, *8*(4), 418–420. doi:10.1038/nn1425

Lacquaniti, R., & Caminiti, R. (1998). Visuo-motor transformations for arm reaching. *European Journal of Neuroscience*, *10*, 195–203. doi:10.1046/j.1460-9568.1998.00040.x

Milner, A. D., & Goodale, M. A. (1998). *The visual brain in action*. Oxford: Oxford University Press. doi:10.1093/acprof:oso/9780198524724.001.0001

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. *Brain*, *111*, 643–674. doi:10.1093/brain/111.3.643

Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia*, *44*, 2734–2748. doi:10.1016/j.neuropsychologia.2006.03.027

Ratcliff, G., & Davies-Jones, G. A. B. (1972). Defective visual localization in focal brain wounds. *Brain*, *95*, 49–60. doi:10.1093/brain/95.1.49

Spiegel, M. A., Koester, D., & Schack, T. (2013). The functional role of working memory in the (re-)planning and execution of grasping movements. *Journal of Experimental Psychology*, *39*(5), 1326–1339. doi:10.1037/a0031398

Tresilian, J. R., & Stelmach, G. E. (1997). Common organization for unimanual and bimanual reach-to-grasp tasks. *Experimental Brain Research*, *115*, 283–299. doi:10.1007/PL00005697

Vindras, P., Blangero, A., Ota, H., Reilly, K., Rossetti, Y., & Pisella, L. (2016). The pointing errors in optic ataxia reveal the role of "peripheral magnification" of the PPC. *Frontiers in Integrative Neuroscience*, *10*(27), 1–17. doi:10.3389/fnint.2016.00027

Witney, A. G. (2004). Internal models for bi-manual tasks. *Human Movement Science*, *23*(5), 747–770.