Direct-effects and after-effects of visuomotor adaptation with one arm on subsequent performance with the other arm

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Wang J, Lei Y. Direct-effects and after-effects of visuomotor adaptation with one arm on subsequent performance with the other arm. *J Neurophysiol* 114: 468–473, 2015. First published May 27, 2015; doi:10.1152/jn.00298.2015.—Adapting to a novel sensorimotor condition is generally thought to result in the formation of an internal representation associated with the novel sensorimotor transform. While the presence of after-effects following sensorimotor adaptation is taken as evidence that such an internal representation was developed as a result of adaptation, it remains unclear whether the absence of after-effects following sensorimotor adaptation indicates that no internal representation was developed. In the present study, we examined this question by having individuals adapt to a 30° visual rotation with one arm first and testing 1) how the initial adaptation would influence subsequent performance with the other arm under the same visual condition (called direct-effects) or under a normal visual condition (called after-effects); and 2) how the initial adaptation that occurred at one workspace location would influence subsequent performance at another location with the same arm under the same or a normal visual condition. Results indicated that initial adaptation with one arm significantly influenced subsequent performance with the other in terms of direct- but not after-effects and that initial adaptation at one workspace location significantly influenced subsequent performance at a new location with the same arm in terms of both direct- and after-effects, but to different extents. These findings indicate that formation of a neural representation associated with a novel visuomotor transform does not always result in after-effects and suggest that visuomotor adaptation may involve multiple aspects of a neural representation, some of which are effector independent and some of which are effector dependent.

WHEN AN INDIVIDUAL EXPERIENCES a novel sensorimotor condition, such as a rotated visual display or a velocity-dependent force field, during targeted reaching movements, his or her hand-paths are largely curved upon initial exposure to the novel condition, but become relatively straight with repeated reaching performances under the same condition. Following complete adaptation, however, these hand-paths become largely curved again, but in the opposite direction, when he or she performs reaching movements under a normal sensorimotor condition. Such “after-effects” are thought to reflect a neural representation, or an internal model, which is associated with a novel sensorimotor transform (Block and Celnik 2013; Heuer and Hegele 2008; Kagerer et al. 1997; Shadmehr and Mussa-Ivaldi 1994).

While the presence of after-effects is considered as evidence for the formation of an internal model, it is uncertain whether the absence of after-effects following sensorimotor training necessarily indicates that no internal model was developed at the end of training. Such an assumption (i.e., no after-effects indicate no internal models) was used in a series of studies conducted by Hodges and colleagues (e.g., Larssen et al. 2012; Lim et al. 2014; Ong and Hodges 2010), in which observers who watched a model adapting to a novel visuomotor condition demonstrated substantial improvement in performance when they later performed a reaching task under the same visuomotor condition (referred to as “direct-effects”), but failed to demonstrate after-effects under a normal visuomotor condition. Based on these findings, Hodges and colleagues suggested that observational learning, which has been suggested to lead to the formation of an internal model (Brown et al. 2010; Mattar and Gribble 2005), may not actually involve an internal model, and that physical practice may be required for the formation of an internal model.

While the studies reported by Hodges and colleagues were controlled very well, the conclusions made by these authors seem to rely heavily on the assumption that no internal model is developed following sensorimotor training unless after-effects are present. However, there is no direct evidence that provides support for this assumption. In fact, our previous experience with studies that investigated interlimb transfer of sensorimotor adaptation suggests that typical sensorimotor adaptation that is acquired by physical practice does not always result in after-effects. For example, we have repeatedly observed the direct-effects of visuomotor adaptation with one arm on subsequent performance with the other arm (e.g., Lei and Wang 2014; Sainburg and Wang 2002; Wang and Sainburg 2006), although we often failed to observe after-effects in similar conditions that involved interlimb transfer (unpublished observations). The direct-effects observed in our studies indicate that initial visuomotor adaptation with one arm led to the formation of an internal model, because these effects are not influenced by the participants’ cognitive awareness (Wang et al. 2011; also see Taylor et al. 2011). These findings and observations indicate that the aforementioned assumption may not be correct; more importantly, they also indicate that conclusions from a study could differ markedly, depending on whether they were based on direct- or after-effects data (e.g., substantial interlimb transfer based on direct-effects, no transfer based on after-effects).

Our arguments stated above, however, are based partly on our published data and partly on our unpublished data. The main objective of the present study, thus, was to examine both the direct- and after-effects of visuomotor adaptation with one arm on subsequent performance with the other arm within a single study. We predicted that, following initial visuomotor

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adaptation with one arm, participants would demonstrate direct-effects, but not after-effects, during subsequent performance with the other arm. Such a finding would indicate that the direct- and after-effects reflect different aspects of a neural representation associated with a novel visuomotor transform. The secondary objective of the present study was to examine the direct- and after-effects of visuomotor adaptation at one workspace location with one arm on subsequent performance at another workspace location with the same arm. This objective was included to determine whether the patterns of direct- and after-effects following visuomotor adaptation would be influenced by the motor effectors involved (i.e., transfer across the arms vs. transfer across conditions within the same arm). We predicted that the patterns of direct- and after-effects would vary, depending on whether they were examined under an interlimb or an intralimb condition. Such a finding would indicate that visuomotor adaptation involves multiple aspects of a neural representation that are either effector independent or effector dependent, which may be reflected differently by the direct- and after-effects.

MATERIALS AND METHODS

Subjects. Subjects were 24 neurologically intact young adults (18-30 yr old, right-handed, 9 women). Their handedness was assessed using the 10-item version of the Edinburgh inventory. All subjects were naive to the purpose of the study and were paid for their participation. Informed consent approved by the Institutional Review Board of the University of Wisconsin-Milwaukee was solicited before participation. Subjects were randomly assigned to one of four groups (6 subjects per group).

Apparatus. A bilateral robotic exoskeleton called KINARM (BKI Technologies, Kingston, ON, Canada) was used to collect movement data. Subjects were seated on the KINARM chair facing a table with both arms supported horizontally. The KINARM was incorporated with a virtual reality system that projected visual targets on a horizontal display to make them appear in the same plane as the arm. Direct vision of the subjects’ hand and arm was blocked by the display, and a cursor representing the index fingertip was projected onto the display to guide their planar reaching movement. The two-dimensional position of arm segments was sampled at 1,000 Hz, low-pass filtered at 15 Hz, and differentiated to yield resultant velocity values. Data were processed and analyzed using MATLAB (The Mathworks, Natick, MA).

Experimental design. In general, subjects performed rapid reaching movements from a start circle to one of eight targets (2 cm in diameter, 10 cm away from the start circle, 30 cm between the left and the right start circles) presented in a pseudorandom sequence on a horizontal tabletop, such that each direction appeared once in eight consecutive trials (Fig. 1A). They were instructed to move their index finger to the target rapidly and as straight as possible in response to the appearance of the target, and stop without correcting their movement. The subjects were divided into four experimental conditions: between-limb/direct-effects (BL/DE), between-limb/after-effects (BL/AE), within-limb/direct-effects (WL/DE), and within-limb/after-effects (WL/AE). For those in the between-limb (BL) conditions, the experiment consisted of three sessions: familiarization with the left arm first, then with the right arm; visuomotor adaptation with the left arm (training); and subsequent performance with the right arm (testing). Each session consisted of 80 (40 with the left, 40 with the right arm), 192 and 192 trials, respectively. In the baseline session, the subjects were familiarized with the general reaching movement with unperturbed visual feedback. In the training session, they adapted to a visual display that was rotated 30° counterclockwise about the start circle (i.e., hand movement made in the “12 o’clock” direction resulted in cursor movement made in the “11 o’clock” direction) with the left arm (Fig. 1B). In the testing session, they performed reaching movements with the right arm either under the 30° rotation condition (DE), or under a condition in which no visual rotation was provided (AE). Continuous visual feedback (in the form of a cursor) was provided throughout the movement in the baseline, training and testing sessions.

Transfer of visuomotor adaptation was only investigated in one direction (i.e., from the left to the right arm), because we assumed based on our previous studies that the pattern of interlimb transfer would be similar regardless of its direction. It has been previously demonstrated that the extent and the rate of visuomotor adaptation are similar between the arms and that transfer of visuomotor adaptation, in terms of directional control, does not vary significantly depending on the direction of transfer when each arm adapts to a rotated display at its ipsilateral workspace (Wang 2008; Wang and Sainburg 2006).

For the subjects in the within-limb (WL) conditions, the experimental procedure was identical to that for those in the BL conditions, except that they performed reaching movements only with the left arm during the familiarization session (40 trials only), and with the left arm during the testing session. The workspace location for the left arm performances during the training session was the same across all experimental conditions, and the workspace location for either the left or the right arm performances during the testing session was the same across all experimental conditions (see Fig. 1A).

Data analysis. To examine performance accuracy, we calculated hand direction error, which was the angular difference between a vector from the start circle to the target and another vector from the hand position at movement start to that at peak arm velocity (i.e., maximum velocity value in a given trial). Hand direction errors obtained from the training and the testing sessions were adjusted based on those errors from the familiarization session for each arm for

![Fig. 1. A: experimental setup. One of 8 targets was displayed at the left workspace location during the training session, and at the right workspace location during the testing session. B: during the training and testing sessions, visual display of the cursor representing fingertip location was rotated 30° counterclockwise. This caused the cursor to move in the −30° direction and the hand in the 0° direction upon initial exposure to the rotation; following complete adaptation, the cursor moved in the 0° direction and the hand in the 30° direction.](http://jn.physiology.org/doi/abs/10.1152/jn.00298.2015)
each subject. Specifically, the direction errors from the training or the testing session subtracted by the mean of the last two cycles (a cycle consists of eight consecutive trials) of direction errors from the familiarization session were used as adjusted hand direction errors. This adjustment allowed us to see easily how close the performances observed during the training and testing sessions were to the baseline performance. For statistical analysis, adjusted hand direction errors from the training and the testing sessions were subjected to a repeated-measures ANOVA with group (BL/DE, BL/AE, WL/DE, WL/AE) as a between-subjects factor and cycle (cycles 1 and 24 of the training session, cycles 1 and 24 of the testing session) as a within-subjects factor. In addition, adjusted hand direction errors from trial 1 of the testing session were subjected to a simple ANOVA with group as a between-subjects factor. The α-level was set at 0.025 (i.e., 0.05/2) for the two ANOVAs after a Bonferroni correction was made, and at 0.05 for post hoc comparisons (Tukey’s tests for between-group comparisons, Fisher’s least significant difference tests for within-group comparisons).

RESULTS

Figure 2 illustrates the cursor-paths of a representative subject from each of the four groups. Their cursor-paths are largely curved at the beginning of the left-arm training session (left panel), which become much straighter by the end of the session (middle panel). At the beginning of the testing session in which the visual rotation was provided (right panel, rows 1 and 2), the cursor-paths from the BL/DE condition are still curved, although they appear to be more accurate than those observed at the beginning of the training session, indicating some transfer from the training to the testing session, and the cursor-paths from the WL/DE condition appear to be as straight and accurate as those observed at the end of the training session, indicating substantial transfer. With respect to the testing session in which no visual rotation was provided (right panel, rows 3 and 4), the cursor-paths from the BL/AE condition were relatively straight and accurate at the beginning of the session, indicating the absence of after-effects, and those from the WL/AE condition were largely curved in the direction opposite to that observed during the training session, indicating substantial after-effects.

Figure 3A depicts changes in performance across trials during the training and testing sessions for each subject group, and Fig. 3B depicts mean direction errors for cycles 1 and 24 of the training session and for cycle 1 of the testing session. The mean direction errors from the three cycles and also from cycle 24 of the testing session were subjected to a repeated-measures ANOVA, which showed a significant interaction effect between group and cycle [F(9,60) = 19.42, P = 0.0001]. This indicates that the pattern of changes in performance across the four cycles was significantly different among the four subject groups. Post hoc within-group comparisons within each subject group, using Fisher’s least significant difference tests, revealed that the improvement from cycle 1 to cycle 24 within the training session was significant in all subjects groups (P < 0.05), which indicates that substantial adaptation occurred during the training session in all groups (Fig. 3B). In addition, a significant difference between cycle 1 of the training session and cycle 1 of the testing session was observed in all groups (P < 0.05), except the BL/AE group, and a significant difference between cycle 24 of the training session and cycle 1 of the testing session was observed in all groups (P < 0.05), except the WL/DE group. Between-group comparisons, using Tukey’s tests, showed that there was no significant difference between any two groups at cycle 1 or 24 during the training session. At cycle 1 of the testing session, however, significant differences were observed between the BL and WL groups in terms of both DE and AE, and also between DE and AE within the BL or the WL group (P < 0.05). These results collectively indicate that between-limb transfer results in significant, but partial, direct-effects and no after-effects, and that within-limb transfer results in complete direct-effects and significant, but partial, after-effects.

Figure 3C depicts changes in performance across trials 1–8 and 185–192 during the training session and trials 1–8 during testing sessions for each subject group. The hand direction errors from trial 1 of the testing session were subjected to a simple ANOVA, which showed a significant group effect [F(3,20) = 9.52, P = 0.0001]. Post hoc between-group comparisons, using Tukey’s tests, showed that there was a significant difference between the BL/DE and the WL/DE groups, and also between the BL/AE and the WL/AE groups (P < 0.05). However, no difference was observed between DE and AE within the BL or the WL group. These results indicate that the direction errors at trial 1 of the testing session are different, depending on whether the same arm was used for both the training and testing sessions or not, although they do not vary, depending on whether the errors were examined in the form of direct- or after-effects.

To ensure that movement duration had no influences on the significant effects reported above, mean duration values from four cycles (cycles 1 and 24 from the training session, cycles 1 and 24 from the testing session) were also obtained from each
subject group and were subjected to another repeated-measures ANOVA with group as a between-subjects factor and cycle as a within-subjects factor. The mean duration values varied between 436 ± 131 and 531 ± 190 ms across the four cycles in the BL/DE group; between 346 ± 165 and 470 ± 111 ms in the BL/AE group; between 398 ± 231 and 495 ± 100 ms in the WL/DE group; and between 431 ± 133 and 485 ± 237 ms in the WL/AE group. The results indicated that neither interaction nor main effects were statistically significant ($P = 0.488$ for cycle, 0.811 for group, 0.828 for group × cycle).

**DISCUSSION**

In the present study, we demonstrated that adaptation to a novel visuomotor condition could transfer across the arms when the transfer was reflected in terms of direct-effects, which is consistent with our laboratory’s previous findings (e.g., Lei and Wang 2014; Sainburg and Wang 2002). When the transfer was reflected in terms of after-effects, however, initial adaptation with one arm did not influence subsequent performance with the other arm (i.e., the subjects were able to move their hand straight to the targets), indicating no transfer. Given that substantial transfer was observed across workspace locations within the same arm, regardless of whether the transfer was reflected in terms of direct- or after-effects in this study, we can safely argue that visuomotor adaptation acquired through physical practice with one arm led to the formation of an internal model, although the presence of an internal model did not result in after-effects during subsequent performance with the other arm. These findings not only challenge the assumption that no internal model is developed following sensorimotor adaptation, unless after-effects are present, but also indicate that conclusions from a sensorimotor adaptation study could differ markedly, depending on whether they were made based on direct- or after-effects data. Our post hoc analyses also demonstrated that conclusions from a study of motor learning transfer could differ, depending on whether the extent of transfer was examined based on direction errors from *block 1* or *trial 1* of the testing session. That is, a significant difference was found between the BL/DE and the BL/AE groups and between the WL/DE and the WL/AE groups when the direction errors from *block 1* of the testing session were subjected to our post hoc analyses, but not when the errors from *trial 1* were. These results suggest that when comparing between direct- and after-effects, investigators should decide carefully to use either data from *trial 1* or those from *block 1* of the testing session depending on their research question.

Our post hoc results based on the direction errors from *trial 1* of the testing session further indicated that, although the extent of transfer did not vary, depending on whether the extent was examined in the form of direct- or after-effects (as indicated by the lack of significant differences for the comparisons mentioned above), it varied depending on whether the same arm was used for both the training and testing sessions or not (as indicated by significant differences between the BL/DE and the WL/DE groups and between the BL/AE and the WL/AE groups). We believe this finding suggests that the information obtained during the training session can be used differently by the motor system, depending on whether transfer occurs across different motor effectors or within the same effector. In the BL conditions, it appears that the motor system simply “loads” the available information at *trial 1* of the testing session and performs a reaching movement. Then, based on the feedback from that trial, the system determines whether the information is useful or not. If it is useful (i.e., in the DE condition), the system utilizes it to facilitate performance, thus resulting in interlimb transfer. If the information is not useful (i.e., in the AE condition), however, the system “turns off” the information, thus resulting in no after-effects. In fact, our laboratory has suggested previously that the motor system uses the first few trials of the testing session with one arm to probe whether movement information obtained with the other arm is useful or not (Wang et al. 2015; Wang and Sainburg 2003), and this...
argument is in agreement with the interpretation of our present data.

In the WL conditions, however, the way the motor system utilizes prior information appears to be somewhat different. The system may still be able to either utilize the information or turn it off based on the feedback received from trial 1 of the testing session. However, it takes a long time for the system to completely remove the after-effects (see data for WL/AE, testing session, compared with data for BL/AE, testing session, in Fig. 3A). These data indicate that the information obtained during initial training with one arm is used differently by the motor system depending on whether the information is transferred across different effectors or within the same effector. These findings suggest that visuomotor adaptation may involve multiple aspects of a neural representation, some aspects that are effector independent and others that are effector dependent, and these aspects may be reflected differently by direct- and after-effects that are associated with visuomotor adaptation.

We have, in fact, argued previously that visuomotor adaptation involves two types of learning mechanisms: algorithmic learning, which is effector independent, and instance-reliant learning, which is effector dependent. Algorithmic learning refers to a type of learning in which one successively improves a rule-based method of control, and instance-reliant learning to another type of learning in which effector-specific instances are accrued during repeated performances of a motor task and automatically retrieved later to allow fast and automatized performances of the task (Lei and Wang 2014; Wang et al. 2015; Wang and Sainburg 2003). Here, the idea of algorithmic learning is in line with the idea of internal models (e.g., Kagerer et al. 1997; Shadmehr and Mussa-Ivaldi 1994), and the idea of instance-reliant learning is in line with the idea of use-dependent learning (Classen et al. 1998; Diedrichsen et al. 2010) and also somewhat in line with the idea of model-free learning [Haith and Krakauer 2013; we argued previously that instance-reliant learning is a type of model-free learning (Wang et al. 2015)]. We have used these ideas to explain the phenomenon that interlimb transfer of visuomotor adaptation, in terms of direct-effects, is typically very limited compared with intralimb transfer (which has also been observed in the present study). According to the ideas of algorithmic and instance-reliant learning, visuomotor adaptation can transfer across the arms mainly by utilizing algorithmic learning, which is effector independent, but the extent of transfer across the arms is limited because it does not involve instance-reliant learning, which is effector dependent (Lei and Wang 2014). This argument has been supported by our recent study in which we demonstrated that adapting to a visuomotor rotation with one arm, while concurrently performing a reaching task repeatedly with the other arm without providing performance feedback (which prevented visuomotor adaptation with this arm, but allowed instances to be accrued), resulted in nearly complete interlimb transfer (Wang et al. 2015).

Given that we observed direct-effects, but no after-effects, in the interlimb transfer conditions in our present study, we speculate that direct-effects may mainly reflect the effector-independent algorithm associated with visuomotor adaptation, and that after-effects may mainly reflect the effector-specific instances associated with visuomotor adaptation. This, however, may not necessarily mean that direct-effects are exclusively associated with algorithms and after-effects exclusively with instances, because after-effects in the context of interlimb transfer have been observed previously. For example, Block and Celnik (2013) examined after-effects with one arm following initial visuomotor adaptation with the other arm, and observed small, but significant, after-effects. Based on this finding, one may argue that after-effects are not exclusively associated with effector-specific instances. Nonetheless, the same authors reported additional findings that can be considered as evidence to support our idea of algorithmic and instance-reliant learning. In their study, subjects received transcranial direct current stimulation (tDCS) on the trained or untrained hemisphere of the cerebellum or the primary motor cortex (M1). While the stimulation of the right cerebellum caused faster adaptation, none of the stimulation sites affected interlimb transfer in terms of after-effects. It should be noted here that the cerebellum is generally thought to be the neural correlates of internal models (Block and Celnik 2013; Haith and Krakauer 2013), while the M1 is thought to be the neural correlates of use-dependent learning (Diedrichsen et al. 2010), model-free learning (Haith and Krakauer 2013) or instance-reliant learning (Wang et al. 2015). According to our idea that direct- and after-effects may mainly reflect the effector-independent algorithm and the effector-specific instances, respectively, tDCS on the cerebellum may affect interlimb transfer when the transfer is reflected in terms of direct-effects, but not in terms of after-effects. Similarly, tDCS on the M1 may not affect interlimb transfer when training and testing involve two different arms. However, if the instances associated with the arm to be used in the testing session were accrued during the training session, tDCS applied on the M1 contralateral to that arm used during the transfer session might influence interlimb transfer in terms of after-effects.

This speculation is somewhat in agreement with the findings reported in the study by Taylor et al. (2011) in which they examined after-effects with one arm following initial visuomotor adaptation with the other arm. The authors observed after-effects in the first few trials of the transfer session, but not in the first cycle (experiment 3, blocked abrupt group), which is consistent with our current results (i.e., the data from BL/AE condition). However, when subjects performed reaching movements with one arm while concurrently adapting to a visuomotor rotation with the other arm (experiment 1, abrupt group), which allowed the instances associated with the arm to be used in the transfer session to be accrued during the training session, the extent of interlimb transfer reflected by after-effects increased substantially. These findings clearly provide support to the idea that effector-specific instances are associated with after-effects following visuomotor adaptation.

In summary, our present findings indicate that formation of a neural representation associated with a novel visuomotor transform (which may not be the same as an “internal model”) does not always result in after-effects. The findings further suggest that visuomotor adaptation may involve multiple aspects of a neural representation, some of which are effector independent (and may involve an internal model), and some of which are effector dependent (and may involve some sort of model-free learning). The nature of these effector-independent and effector-specific aspects of a neural representation remains to be further investigated.

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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS
Author contributions: J.W. and Y.L. conception and design of research; J.W. interpreted results of experiments; J.W. and Y.L. prepared figures; J.W. drafted manuscript; J.W. and Y.L. edited and revised manuscript; J.W. approved final version of manuscript; Y.L. performed experiments; Y.L. analyzed data.

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