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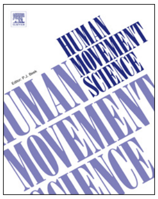

Full Length Article

Direct-effects and after-effects of dynamic adaptation on intralimb and interlimb transfer

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ABSTRACT

After-effects following sensorimotor adaptation are generally considered as evidence for the formation of an internal model, although evidence lacks on whether the absence of after-effects necessarily indicates that the adaptation did not result in the formation of an internal model. Here, we examined direct- and after-effects of dynamic adaptation with one arm at one workspace on subsequent performance with the other arm, as well as the same arm at another workspace. During training, subjects performed reaching movements under a novel dynamic condition with the right arm; during testing, they performed reaching movements with the left or right arm at a new workspace, under either the same dynamic condition (direct-effects) or a normal condition (after-effects). Results showed significant transfer within the same arm in terms of both direct- and after-effects, but significant transfer across the arms only in terms of direct-effects. These findings suggest that the formation of an internal model does not always result in after-effects. They also support the idea that the neural representation developed after sensorimotor adaptation comprise some aspects that are effector independent and other aspects that are effector dependent; and that direct- and after-effects following sensorimotor adaptation mainly reflect the effector-independent and the effector-dependent aspects, respectively.

1. Introduction

Designing effective rehabilitation protocols for those with motor impairment, such as stroke survivors, requires comprehensive understanding of how the brain acquires and executes movement (Krakauer, 2006). Stroke in humans typically results in abnormal coordination between the shoulder and elbow joint (Beer, Dewald, Dawson, & Rymer, 2004; Dewald, Sheshadri, Dawson, & Beer, 2001), significantly compromising daily life activities such as drawing and reaching. One possible way to modify pathological patterns of inter-joint coordination is to use adaptation paradigms that help stroke patients to converge on desire behaviors. To understand this, previous studies considered adaptation of the nervous system to novel sensorimotor conditions, and how such adaptation generalizes across different situations in neurologically intact individuals. Those studies generally demonstrated that hand-paths during arm reaching movements were perturbed greatly upon initial exposure to a novel sensorimotor condition, regardless of whether the perturbation was due to a novel visuomotor (e.g., Krakauer, Pine, Ghilardi, & Ghez, 2000; Taylor, Wojaczynski, & Ivry, 2011; Wang, Joshi, & Lei, 2011; Wang & Sainburg, 2005) or dynamic condition (e.g., Joiner, Brayanov, & Smith, 2013; Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994; Stockinger, Focke, & Stein, 2014; Wang, Lei, Xiong, & Marek, 2013); and that they became relatively straight by the end of a training session, indicating adaptation to the novel sensorimotor condition.

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Many studies also demonstrated that following sensorimotor adaptation, abrupt removal of the perturbation resulted in a deviation in the subject's hand-path, albeit in the opposite direction. These deviations, known as 'after-effects' are generally considered as evidence for successful motor adaptation and, thus, for the formation of an internal model associated with the novel sensorimotor transform (Heuer & Hegele, 2008; Kagerer, Contreras-Vidal, & Stelmach, 1997; Shadmehr & Mussa-Ivaldi, 1994; Shadmehr, Smith, & Krakauer, 2010). It is generally accepted that internal models are encoded in the cerebellum (Ito, 1970; Kawato, 1999; Wolpert, Ghahramani, & Jordan, 1995; Wolpert, Miall, & Kawato, 1998), as evidenced by findings from electrophysiological studies, which, for example, have demonstrated that the discharge of Purkinje cells in the cerebellum of non-human primates reflects the output of an internal model (Herzfeld, Kojima, Soetedjo, & Shadmehr, 2015; Popa, Hewitt, & Ebner, 2012) or by findings from behavioral studies, which, for example, have revealed that humans with cerebellar dysfunction have general difficulties in adaptation to both visuomotor (Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007) and dynamic (Gibo, Criscimagna-Hemminger, Okamura, & Bastian, 2013; Maschke, Gomez, Ebner, & Konczak, 2004) perturbations.

The absence or presence of after-effects following sensorimotor training is commonly used in research to determine whether motor adaptation has occurred or not following training (e.g., Lim, Larssen, & Hodges, 2014; Ong & Hodges, 2010; Shadmehr & Brashers-Krug, 1997). Nevertheless, evidence lacks on whether the absence of after-effects necessarily indicates that sensorimotor training did not result in the formation of an internal model associated with the given sensorimotor transform. Research in interlimb transfer of visuomotor adaptation in our lab has shown that initial adaptation to a novel visuomotor condition with one arm typically results in significant reduction of performance errors during subsequent adaptation to the same condition with the opposite arm. These observed 'direct-effects' suggest that the initial training with the first arm resulted in the formation of an internal model, which in turn was utilized to facilitate subsequent adaptation with the other arm (e.g., Lei & Wang, 2014; Wang & Sainburg, 2003, 2004; Wang et al., 2011). However, after-effects are not always observed under similar interlimb transfer conditions. For example, we recently demonstrated that initial adaptation to a novel visuomotor condition with one arm resulted in after-effects during subsequent performance under a normal visuomotor condition with the same arm, which indicates that an internal model was formed following the adaptation. The initial adaptation, however, did not result in after-effects when the other arm was used during subsequent performance under a normal visuomotor condition (Wang & Lei, 2015). These findings suggest that whereas the presence of after-effects may serve as evidence for the formation of an internal model, its absence does not necessarily indicate that no internal model was formed following a given visuomotor adaptation.

While our previous study (Wang & Lei, 2015) demonstrates that an internal model obtained following *visuomotor* adaptation is not always accompanied by after-effects, it remains to be seen whether it is also the case following *dynamic* adaptation. Indeed, it has been suggested that adaptation to visual and dynamic perturbations involve distinct neural mechanisms (e.g., Krakauer, Ghilardi, & Ghez, 1999; Wang & Sainburg, 2004). This suggestion is in agreement with neurophysiological findings, which demonstrated that neural processes underlying adaptation to visual and dynamic perturbations involved different cerebellar structures: visuomotor adaptation mainly involved the posterior lobe (i.e., lobule VI), and dynamic adaptation mainly the anterior lobe (i.e., lobules IV and V) (Donchin et al., 2012; Rabe et al., 2009). Moreover, it is known that visual adaptation mainly depends on visual input (Krakauer et al., 2000), while proprioceptive information is critical for dynamic adaptation (Bock & Thomas, 2011; Hwang & Shadmehr, 2005; Pipereit, Bock, & Vercher, 2006). Therefore, the aim of the present study was to investigate both the direct- and after-effects of adaptation to a velocity-dependent force field with one arm on subsequent performance with the other arm, as well as on subsequent performance with the same arm in another workspace. Previous studies typically examined either the direct-effects or the after-effects of dynamic adaptation on interlimb (or intralimb) transfer, but not both within the same study.

2. Methods

2.1. Subjects

Twenty-four neurologically intact, right-handed young adults (18–30 years old, 8 males) were recruited from the University of Wisconsin-Milwaukee community. Subjects signed an informed consent approved by the Institutional Review Board of the university prior to participation. Subjects were randomly assigned to one of four groups (six subjects per group).

2.2. Apparatus

Movement data were collected using a bilateral robotic exoskeleton called KINARM (BKIN Technologies, Kingston, ON, Canada). Subjects sat on the KINARM chair with their arms supported on the exoskeleton that provided full gravitational support of the entire arms. The chair was then moved to bring the arms under a horizontal display. A virtual reality system was built in the KINARM, which projected visual targets on the display to make them appear in the same plane as the arms. After calibration, direct vision of the subjects' arm was blocked, and a cursor representing their index fingertip was provided to guide their reaching movement. The two-dimensional position data of the hand were sampled at 1000 Hz, low-pass filtered at 15 Hz, and differentiated to yield resultant velocity values. Data were processed and analyzed using MATLAB (The Mathworks Inc., Natick, MA).

2.3. Experimental procedures

The experiment consisted of rapid, outward reaching movements from a start circle (1 cm in diameter) to one of eight targets (1 cm in diameter) that were presented in a pseudorandom sequence within each cycle (i.e., eight consecutive trials including all

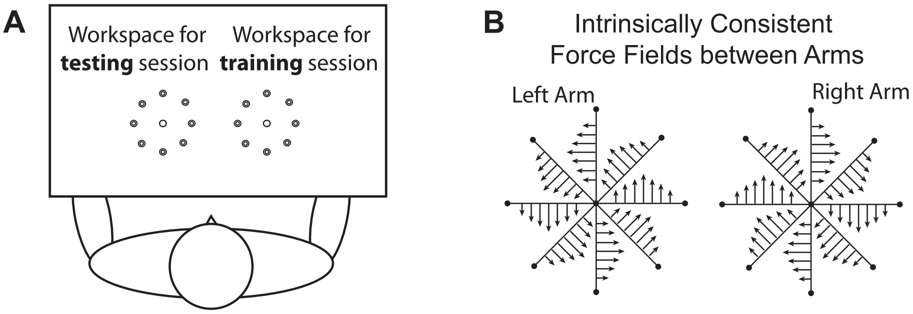

Fig. 1. (A) Experimental setup. One of 8 targets was displayed at the right workspace location during the training session, and at the left workspace location during the testing session. (B) Direction of the velocity-dependent force field applied to each arm during reaching movement. Longer arrows indicate greater forces. Force directions were intrinsically consistent between the arms (BL/DE condition).

target directions) (Fig. 1A). The distance between the start circle and each target was 10 cm. Subjects were instructed to reach in a straight and fast motion toward the targets. Movements were required to have a reaction time (RT) of < 600 ms and a movement time (MT) within 400–800 ms. The color of the target turned red or blue if the movement speed was too fast or too slow, respectively. The target color was green when the performance met the MT requirement. The time constraints were imposed to minimize variability in movement speed across trials and across subjects. After reaching the target, the subjects were instructed to bring the hand back to the start circle. (Data were not collected during the movements back to the start circle.)

Four experimental conditions were examined: 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). Each condition consisted of three sessions: familiarization, training, and testing. The familiarization session (in the BL conditions: 40 trials for each arm; in the WL conditions: 40 trials for the right arm only) aimed to familiarize the subjects with the general reaching movements made in the eight target directions.

To examine adaptation to a novel dynamic condition, a velocity-dependent endpoint force field (fx, fy) was mimicked using the motors of the robotic exoskeleton as follows:

$$\begin{bmatrix} \mathrm{fx} \\ \mathrm{fy} \end{bmatrix} = \begin{bmatrix} 0 & k \\ -k & 0 \end{bmatrix} \begin{bmatrix} \mathrm{vx} \\ \mathrm{vy} \end{bmatrix}$$

where $k = 15\,\mathrm{N/(m/s)}$; vx and vy are the x- and y-components of the endpoint velocity (m/s), respectively. This force field was on during reaching movements toward the target and off during reaching movements back to the start circle. The force field was provided to the right hand during the training session in all four groups; to the left hand during the testing session in the BL/DE group; and to the right hand during the testing session in the WL/DE group. Both the training and the testing sessions consisted of 192 trials.

In this study, interlimb transfer of dynamic adaptation was examined from the right to the left arm, because previous studies typically demonstrated significant transfer in this direction (e.g., Carroll, De Rugy, Howard, Ingram, & Wolpert, 2016; Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Galea, Miall, & Woolley, 2007; Stockinger, Thürer, Focke, & Stein, 2015; Wang & Sainburg, 2004). In addition, we decided to use intrinsically consistent (i.e., mirror-imaged) force fields between the arms in the BL/DE condition (Fig. 1B), because our preliminary data (i.e., data obtained from three subjects tested with extrinsically consistent force fields between the arms vs. those from three subjects tested with intrinsically consistent force fields) indicated greater transfer using intrinsically, as compared to extrinsically, consistent force fields between the arms.

While the training session was identical for all four groups (i.e., the right arm used in its ipsilateral workspace), the testing session differed for each group: the subjects in the BL groups performed reaching movements with the left arm under the force field condition that was mirror-imaged to the condition they experienced during the training session (BL/DE) or without the force field present (BL/AE); and those in the WL groups performed reaching movements with the right arm under the force field condition that was the same as the condition they experienced during the training session (WL/DE) or without the force field present (WL/AE). The workspace location used during the testing session was always the same (i.e., a workspace location on the left side from midline; see Fig. 1A) regardless of the groups. The sequence of the targets presented was the same for all subjects, and also for the training and testing sessions (e.g., the same target direction was provided at the first trial in both sessions). Visual feedback of the cursor representing the index finger tip was available throughout the experiments.

2.4. Statistical analysis

To examine performance accuracy, we calculated 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. Direction errors obtained from the training and the testing sessions were adjusted based on those errors from the familiarization session for each arm for each subject. Specifically, the direction errors from the training or the testing session subtracted by the mean of the last two cycles of direction errors from the familiarization session were used as adjusted hand direction errors. This adjustment allowed us to see

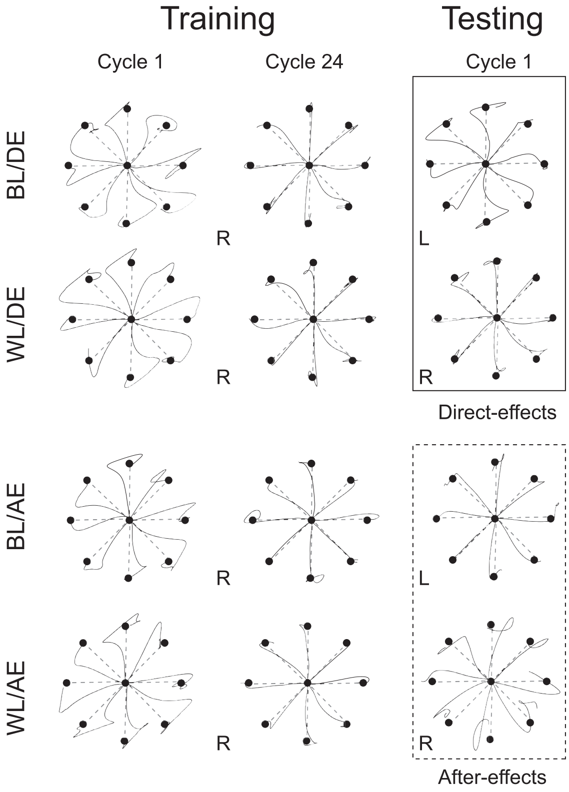

Fig. 2. Hand-paths from a representative subject from each of four experimental conditions. Hand-paths in columns 1 and 2 represent the first and the last 8 consecutive trials observed during the training session, respectively; hand-paths in column 3 represent the first 8 consecutive trials observed during the testing session. Hand-paths shown inside the solid box indicate reaching movements performed under the force field condition (reflecting direct-effects); hand-paths inside the broken box indicate those under a normal condition (reflecting after-effects). Hand-paths performed with the right arm are marked with 'R'; those performed with the left arm are marked with 'L'. Solid lines represent the hand-paths from each experimental condition; broken lines represent ideal straight hand-paths from start circle to targets.

easily how close the performances observed during the training and testing sessions were to the baseline performance.

For statistical analysis, adjusted direction errors (call 'direction errors' henceforth) 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 (the first and the last cycles of the training session, the first cycle of the testing session) as a within-subjects factor. In addition, direction errors from trial 1 of the testing session were subjected to a simple ANOVA with Group as a between-subjects factor. The alpha level was set at 0.025 (i.e., 0.05/2) for the ANOVAs after a Bonferroni correction was made, and at 0.05 for post hoc comparisons (Tukey's tests for between-group comparisons, Fisher's LSD tests for within-group comparisons).

3. Results

Hand-paths of a representative subject from each subject group are depicted in Fig. 2. Regardless of the condition, subjects' hand-paths were largely curved at the beginning of the training session (left panel, solid line), which became relatively straight by the end of the session (middle panel, solid line). During the testing sessions in which the force field was present (right panel, solid line), hand-paths of the subjects in the BL/DE condition (row 1) continued to be deviated, although they appear to be considerably straighter than those observed at the beginning of the training session, indicating some transfer of dynamic adaptation from the right to the left arm. In contrast, the hand-paths of those tested in the WL/DE condition were much straighter and appear quite similar to those observed at the end of the training session, indicating substantial transfer across the two workspace locations. With respect to the hand-paths observed during the testing sessions in which the force field was not present (right panel, solid line), those of the subjects tested in the BL/AE condition (row 3) were relatively straight to the targets, indicating the absence of after-effects, whereas those from the WL/AE condition (row 4) showed large deviations that were in the opposite direction to those observed at the beginning of the training session, indicating the presence of after-effects.

Fig. 3A shows changes in direction errors across the entire trials during the training and testing sessions for each subject group; and Fig. 3B shows the direction errors at the first and the last cycles of the training session, as well as those at the first cycle of the testing session. The repeated-measures ANOVA, with Group (BL/DE, BL/AE, WL/DE, WL/AE) and Cycle (the first and the last cycles of the training session, the first cycles of the testing session) as a within-subjects factor, showed a significant interaction effect

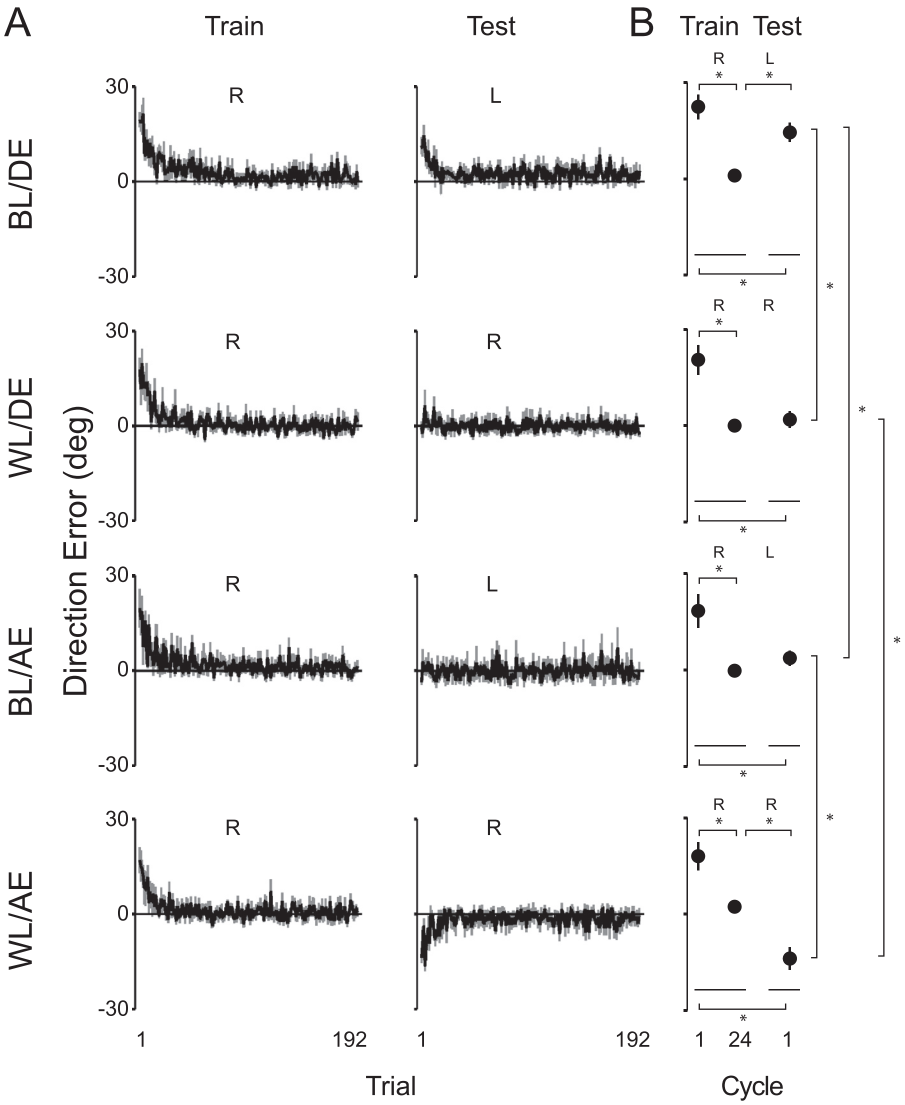

Fig. 3. Changes in direction errors (mean and standard errors) during the training and testing sessions. (A) Performance changes are shown across trials 1–192 for training and testing sessions separately for each subject group. Thick black lines indicate mean direction errors; grey lines indicate SE. (B) Direction errors are shown for first and last cycles of training session and for first cycle of testing session. Thin horizontal lines indicate post hoc comparisons between the given two cycles within each subject group, and thin vertical lines post hoc comparisons between the given two subject groups for first cycle of testing session ($^{*} < .05$).

between Group and Cycle ($p < 0.001$), indicating that the pattern of performance changes across the three cycles was significantly different among the four subject groups. Post hoc within-group comparisons revealed that the improvement from the first to the last cycle during the training session was significant in all subject groups ($p < 0.01$), which indicates that substantial adaptation occurred during the training session in all groups. In addition, a significant difference between the last cycle of the training session and the first cycle of the testing session was observed in the BL/DE and WL/AE groups ($p < 0.01$); and a significant difference between the first cycle of the training session and the first cycle of the testing session was observed in all groups ($p < 0.05$). As illustrated in Fig. 3A, these data indicate the following: (1) in the BL/DE group, a significant, but limited transfer of dynamic adaptation occurred from the right to the left arm in terms of direct-effects; (2) in the WL/DE group, a significant, and nearly complete transfer occurred from the right to the left workspace location (within the right arm) in terms of direct-effects; (3) in the BL/AE group, no transfer occurred from the right to the left arm at all in terms of after-effects; and (4) in the WL/AE group, a significant transfer occurred from the right to the left workspace location (within the right arm) in terms of aftereffects.

We also conducted post hoc comparisons between every two subject groups (e.g., BL/DE vs. WL/DE, BL/DE vs. BL/AE) using the direction errors at the first cycle of the testing session, which indicated that the size of direction error at the first cycle of the testing session varied between the DE and the AE conditions, and also between the BL and the WL conditions ($p < 0.05$). The simple ANOVA using direction errors at the first trial of the testing session also showed a significant effect of Group ($p < 0.01$), and post hoc comparisons indicated the same pattern of data (i.e., significant differences between the DE and the AE conditions, and also between the BL and the WL conditions ($p < 0.05$).

4. Discussion

In the present study, our data from the between-limb conditions indicated that initial adaptation with one arm resulted in a significant, but limited transfer, thus facilitating subsequent performance with the other arm under the same dynamic condition (BL/DE); whereas the initial adaptation had no influence in subsequent performance with the other arm under the null force-field condition (BL/AE). These data indicate clearly that transfer of dynamic adaptation occurred across the arms in terms of direct-effects, but not in terms of after-effects. With respect to the data from the within-limb conditions, initial adaptation at one workspace location resulted in nearly complete transfer, facilitating subsequent performance at a different workspace location substantially when the force field was present at both workspace locations (WL/DE). When the force field was removed during the testing session (WL/AE), transfer did occur in terms of after-effects. These results indicate that transfer of dynamic adaptation occurred across the workspaces within the same arm in terms of not only direct-effects, but also after-effects.

Our findings from the within-limb conditions are consistent with the findings reported in our previous study in which direct- and after-effects of visuomotor adaptation were investigated (Wang & Lei, 2015). That is, in both studies, initial adaptation to a novel sensorimotor condition (visuomotor in our previous study, dynamic in the current study) transferred across different workspace locations within the same arm in terms of both direct- and after-effects. With respect to the between-limb conditions, our current findings are consistent with those reported in our previous study as well, in that transfer of both visuomotor and dynamic adaptation occurred across the limbs in terms of direct-effects, but not in terms of after-effects. These findings collectively provide support to the argument that whereas the presence of after-effects following sensorimotor adaptation (as in our WL/AE condition) may serve as evidence for the formation of an internal model, its absence (as in our BL/AE condition) does not necessarily indicate that no internal model was formed following the adaptation (Wang & Lei, 2015). Our current findings further indicate that this argument is true regardless of whether the adaptation involves a novel visuomotor or dynamic transformation.

Furthermore, these findings suggest that the direct- and after-effects may reflect different aspects of a neural representation associated with a novel sensorimotor transform. Given that the direct-effects were observed in both the between-limb and the within-limb conditions, they seem to reflect the aspects of a neural representation that are effector independent. In contrast, the fact that the after-effects were only observed in the within-limb conditions seems to indicate that they mainly reflect the aspects that are effector dependent. This interpretation is in agreement with a notion that sensorimotor adaptation involves algorithmic learning, which is effector independent, and instance-reliant learning, which is effector dependent (Bao, Lei, & Wang, 2017; Lei & Wang, 2014; Wang & Lei, 2015; Wang, Lei, & Binder, 2015; Wang & Sainburg, 2003). Algorithmic learning refers to a type of learning in which one successively improves a rule-based method of control; and this idea is in line with the idea of internal models (e.g., Kagerer et al., 1997; Shadmehr & Mussa-Ivaldi, 1994) or model-based learning (Haith & Krakauer, 2013). Instance-reliant learning refers 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; and this idea is in line with the idea of use-dependent learning (Classen, Liepert, Wise, Hallett, & Cohen, 1998; Diedrichsen, White, Newman, & Lally, 2010) and also somewhat in line with the idea of model-free learning (Haith & Krakauer, 2013). With respect to the neural substrates involved in algorithmic and instance-reliant learning, the cerebellum, which is known to be involved in model-based learning (Haith & Krakauer, 2013), is also thought to be involved in algorithmic learning; and the primary motor cortex, which has been suggested to be involved in model-free or use-dependent learning (Diedrichsen et al., 2010; Haith & Krakauer, 2013), is also thought to be involved in instance-reliant learning (Lei, Bao, Perez, & Wang, 2016; Wang et al., 2015). Using the ideas of algorithmic and instance-reliant learning, we have explained previously why interlimb transfer of visuomotor adaptation is typically very limited compared with intralimb transfer (Lei & Wang, 2014), and also how providing motor instances can increase the extent of interlimb transfer substantially (see Wang et al., 2015).

Our findings, however, do 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 following dynamic adaptation have been observed previously. For example, transfer of dynamic adaptation across the arms was observed when it was measured during error-clamp trials (Joiner et al., 2013; Stockinger et al., 2015). Interlimb transfer in the form of after-effects was also observed following adaptation to Coriolis force perturbations (Lackner & Dizio, 1994; Lefumat et al., 2016). Considering all these findings, we speculate that direct-effects may mainly (but not exclusively) reflect the effector-independent algorithm associated with sensorimotor adaptation, and that after-effects may mainly (but not exclusively) reflect the effector-specific instances associated with sensorimotor adaptation. It should be noted, however, that the way after-effects were measured are somewhat different across these studies (i.e., free reaching movements (our current study) vs. reaching movements somewhat constrained within the error-clamp (Joiner et al., 2013; Stockinger et al., 2015) vs. reaching movements following adaptation to Coriolis forces, which possibly had a certain influence in the entire body (Lackner & Dizio, 1994; Lefumat et al., 2016). Further research is needed to determine how these different methods influence the measurement of after-effects.

While our present findings are consistent in many ways with those from our previous study in which transfer of visuomotor adaptation was investigated (Wang & Lei, 2015), some discrepant findings are also observed. In our previous study, we observed that during interlimb transfer, the direction errors at the first trial of the testing session were not significantly different between the direct- and the after-effects conditions, based on which we argued that following initial visuomotor adaptation with one arm, the motor system would use the first few trials to probe whether movement information obtained during initial training was useful or not during subsequent performance with the other arm. If the information was determined useful, the system would utilize the information, thus resulting in transfer (i.e., as in the direct-effects condition); but if determined useless, the system would not, thus resulting in no transfer (i.e., as in the after-effects condition). This idea has also been used to explain similar findings in our previous studies (Wang & Sainburg, 2003; Wang et al., 2015). In the present study, however, the direction errors at the first trial of the testing session were significantly different between the direct- and the after-effects conditions in both the between- and the within-limb conditions.

This discrepancy may be attributed to the fact that different sensory feedback processes are involved in visuomotor versus dynamic adaptation. During visuomotor adaptation, an individual can reduce her performance errors based on the visual feedback provided during a reaching movement, although it takes a substantial amount of time not only to process the visual information, but also to correct her movement voluntarily based on that feedback. During dynamic adaptation, however, performance errors accompany changes in muscle lengths that are transduced by proprioceptive sensors, which in turn evoke short- and long-latency responses (Hwang, Smith, & Shadmehr, 2006). The amount of time required to correct a reaching movement in this case is thought to be much shorter than that to do so based on visual feedback (Gottlieb & Agarwal, 1984). Thus, it is plausible in the present study that the dynamic perturbation provided at the first trial of the testing session in the BL/DE condition caused the muscle lengths to change, which enabled the subjects to adjust their movement very quickly, while such an adjustment was not needed in the BL/AE condition due to the absence of any mechanical perturbation (thus resulting in the difference between the DE and the AE conditions in terms of the direction errors at the first trial of the testing session). In contrast, the visuomotor perturbation provided in our previous study would not enable the subjects to adjust their movements so quickly (thus resulting in the lack of difference between the BL/DE and the BL/AE conditions in terms of the direction errors at the first trial of the testing session). This interpretation is in agreement with the findings reported by Wong, Wilson, Malfait, and Gribble (2009), who demonstrated that individuals would modulate limb stiffness during dynamic adaptation, but not during visuomotor adaptation. Based on this finding, the authors suggested that movement corrections based on visual information alone would not be sufficient to engage neural systems for stiffness control, which might depend on sensory signals more directly related to mechanical perturbations, such as those arising from proprioceptive (and somatosensory) signals.

Finally, it is worth noting that we observed significant transfer of dynamic adaptation across the arms, in terms of direct-effects, in the present study in which we employed intrinsically consistent force fields between the arms. The literature is still inconclusive as to whether interlimb transfer of dynamic adaptation can occur better along intrinsic or extrinsic coordinates. For example, Criscimagna-Hemminger et al. (2003) reported that adaptation to a velocity-dependent force field transferred across the arms along extrinsic, but not intrinsic, coordinates, whereas Wang and Sainburg (2004) demonstrated interlimb transfer of adaptation to an inertial load along intrinsic coordinates. To account for the discrepancy, we argued that the coordinate systems involved in interlimb transfer of dynamic adaptation might depend on a number of factors, such as the type of forces employed (e.g., velocity dependent, acceleration dependent) and the availability of various sensory information (e.g., haptic, vestibular, vision) (Wang & Sainburg, 2004). Thus, at the designing stage of the experiment reported in the present study, we first tested three subjects in the BL/DE condition, in which we employed extrinsically consistent force fields between the arms; and we expected to observe a decent amount of interlimb transfer in

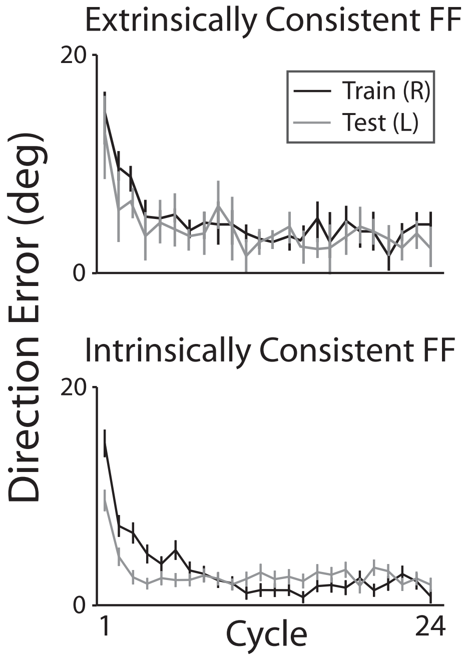

Fig. 4. Transfer of dynamic adaptation across the arms. *Top:* When the force fields were extrinsically consistent, no improvements in performance with the left arm were observed following initial adaptation with the right arm. Bottom: When the force fields were intrinsically consistent between the arms, initial adaptation with the right arm during training session led to noticeable improvements in performance with the left arm during testing session.

that condition, based on the findings reported by Criscimagna-Hemminger et al. (2003). Surprisingly, however, we did not observe interlimb transfer in these subjects (Fig. 4, top), which caused us to test three new subjects in the same condition, but using intrinsically consistent force fields between the arms. The data from the subjects tested using intrinsically consistent force fields, then, clearly indicated interlimb transfer (Fig. 4, bottom). Our data indicate that interlimb transfer of force-field adaptation can occur along either intrinsic (as shown in the present study) or extrinsic (as shown in Criscimagna-Hemminger et al. (2003)'s study) coordinates. This idea is partly in agreement with a notion that internal models do not employ a single coordinate system, but rather employ multiple, simultaneous coordinate systems when generalizing dynamic adaptation across different conditions within the same arm (Berniker, Franklin, Flanagan, Wolpert, & Kording, 2014) or across the arms (Parmar, Huang, & Patton, 2015). Further research is warranted to elucidate factors that determine the type of coordinate systems employed across different generalization conditions.

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