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RESEARCH ARTICLE

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# Inter- and intra-limb generalization of adaptation during catching

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**Abstract** We have previously shown that healthy adults require a few trials to adapt to a changed ball weight during catching. It is not known whether this adaptation generalizes to the opposite arm or to different configurations of the same arm. We tested healthy adult subjects catching balls of different weight while maintaining the hand within a vertical spatial "window." In experiment 1, subjects caught a series of light and heavy balls, first with one hand and then with the other. In experiment 2, subjects caught a series of light and heavy balls, first with the catching arm in either a "bent" or a "straight" configuration and then with the same arm in the other configuration. A percentage transfer value was calculated to determine the degree to which previous experience with a given ball weight in one context affected performance of the same task in a new context (i.e., different arm or different arm configuration). Results showed that generalization occurred both between arms and within an arm. However, the subjects who switched arms showed less generalization than those who switched arm positions. Specifically, the percentage transfer value for subjects who switched arms was 58%, while the percentage transfer for those who switched arm positions was 100%. These results support the idea that the motor system is able to generalize adaptive control of ball catching to the contralateral arm and to different arm configurations. Our findings are also in agreement with the recent notion that multiple internal representations of a task may exist in the CNS. Because there was partial generalization between the two arms, we conclude that there must be a representation stored and used for catching that is not effector specific, but rather can be utilized by brain regions controlling either arm. However, because generalization was only complete within an arm, we conclude that another sensorimotor representation exists, which might only be stored in brain regions specific to a single arm.

**Keywords** Motor · Adaptation · Generalization · Human

## Introduction

Many motor tasks require anticipatory (feedforward) control for successful performance. For example, catching a ball requires anticipatory muscle activity that is scaled to the momentum of the ball (Lacquaniti and Maioli 1989; Bennett et al. 1994). This anticipatory control must also be constantly adjusted to account for the changing task parameters. Thus, a change in ball weight during catching requires a few trials of practice to adapt the motor response (Lang and Bastian 1999, 2001). We have found that the trial dependence of this adjustment does not change even when normal healthy subjects are allowed to feel the weight of the ball prior to catching (Lang and Bastian 2001). This is probably because anticipatory muscle activity is scaled to the expected momentum of the ball, which depends on the drop height as well as the ball weight. Apparently, the visual estimation of drop height and the stored information about ball weight are insufficient to accurately predict momentum.

Another important aspect of motor control is generalization. The extent to which adaptation of a movement can be generalized to other movements within the same limb or between limbs is of significance, particularly as we interact with objects in the environment. Generalization has been demonstrated in a number of different tasks, though the type and extent of generalization varies from study to study (Gordon et al. 1994; Shadmehr and Mussa-Ivaldi 1994; Dizio and Lackner 1995; Gandolfo

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et al. 1996; Martin et al. 1996b; Conditt et al. 1997; Sainburg et al. 1999). Relatively large extents of generalization between arms (inter-limb) can be demonstrated with tasks that are familiar and simple in nature such as grasping and lifting small objects (Gordon et al. 1994). However, incomplete inter-limb generalization may occur during more complex motor tasks such as reaching in the presence of Coriolis forces (Dizio and Lackner 1995). Generalization from one movement to a different movement with the same arm (intra-limb generalization) can also be incomplete in complex motor tasks. For example, adaptation to reaching in viscous force fields (Shadmehr and Mussa-Ivaldi 1994; Gandolfo et al. 1996; Conditt et al. 1997) or with novel inertial loads (Sainburg et al. 1999) both show intra-limb generalization that decays as the movement direction deviates from the trained direction.

Only a couple of studies have compared the extent of inter- and intra-limb generalization using the same task (Martin et al. 1996b; Salimi et al. 2000). Martin and colleagues have studied subjects as they adapt an overhand throwing movement to novel prism glasses and are then tested throwing underhanded or with the other hand. Subjects show very little intra-limb generalization (over- to underhanded) and no inter-limb generalization (arm to arm). Salimi and colleagues have studied anticipatory control of fingertip forces when subjects grasp and lift a novel object with the center of mass shifted to one side. They found that after practice, there is no significant intra-limb generalization when subjects pick up the object after it has been rotated 180° (shifting the center of mass to the other side). No inter-limb generalization is found with the object in either configuration (Salimi et al. 2000).

What determines the extent of generalizability remains unknown, but it is probably due to the nature of the task and subsequent representation in the central nervous system (CNS). Presumably, the information that the brain stores and uses to generate the appropriate motor response varies across these tasks. During some tasks, it has been speculated that the brain creates an internal representation of the appropriate effector (limb) output necessary to successfully perform a skill (Shadmehr and Mussa-Ivaldi 1994; Flanagan and Wing 1997; Thoroughman and Shadmehr 1999). This internal representation may be stored in structures specific to the motor output, and would thus not be expected to generalize to other effectors. Other tasks may require representation of an external parameter specific to the task, such as the physical properties of the object being manipulated (Gordon et al. 1994). Presumably, representation of this parameter could be used to modify the output of any effector, and would thus be expected to generalize to some degree. It is also possible that, for many tasks, both types of information need to be stored.

The purpose of this study was to determine whether the adaptation to novel ball weights that occurs during catching generalized to new contexts. Specifically, we compared the relative extents of generalization across different arms (inter-limb) or across different configurations of the same arm (intra-limb). We found that intra-limb generalization was greater than inter-limb generalization, though both occurred. By and large, subjects only performed the catch correctly on the first trial after switching arm configurations; they rarely performed the catch correctly on the first trial after switching arms. Preliminary results from this study have been published in abstract form (Morton et al. 2000).

## Methods

### Subjects

Seventeen right-handed, healthy adults (14 women and 3 men, age range 23–60 years) participated in the study. Nine subjects (28.22 ± 3.99 years, mean ± SE) participated in experiment 1. A second group of eight subjects (25.00 ± 0.63 years) participated in experiment 2. All subjects gave their informed consent prior to participating, and a Human Studies Committee approved the study.

### Paradigm

The basic paradigm has been described previously (Lang and Bastian 1999). Briefly, all subjects were required to repeatedly catch balls of different weight, but the same size, dropped into the hand from above (Fig. 1a). Subjects caught the ball with their arm in one of two positions. In the "bent" position, subjects held the arm in approximately 10° shoulder flexion, 80° elbow flexion, and 0° wrist flexion. In the "straight" position, subjects held the arm in approximately 80° shoulder flexion, 10° elbow flexion, and 0° wrist flexion. Subjects were instructed to catch the ball while maintaining their hand within a 10-cm vertical spatial "window." A pole was positioned next to the catching hand to mark the top, middle, and bottom of the window. Balls were dropped at the sound of a tone from a 40-cm height directly above the subject's hand. The 40-cm drop height was chosen based on previous works that indicated this height would allow sufficient time for anticipatory muscle activity to occur (Lacquaniti and Maioli 1989; Lang and Bastian 1999).

The balls were made of different colored latex material, all approximately 12 cm in diameter. They were soft and easy to grasp. Subjects repeatedly caught two balls, first a "light" and then a "heavy" ball. The weight of the light ball was either 320 g or 545 g, depending on the subject's size and body weight. The 545-g ball was used with larger, stronger subjects while the 320-g ball was used for smaller subjects. The weight of the heavy ball was either 450 g or 680 g heavier than the light ball, again depending on the subject's size and body weight. The mean weight of the heavy ball did not differ from experiment 1 to experiment 2 ($p > 0.05$).

In experiment 1, we tested inter-limb generalization. Subjects caught balls using the right or left arm, always in the bent position. Subjects completed a baseline phase, an adaptation phase, and a transfer phase. The baseline phase consisted of 8–12 trials catching the light ball, first with either the right or left arm (arm 1) and then with the other arm (arm 2). The purpose of the baseline phase was to familiarize subjects with the task, allow them practice catching the ball with both arms, and to detect any differences attributable to the catching arm. The adaptation phase consisted of 18–22 trials of catching the heavy ball with arm 2. The transfer phase consisted of 18–22 trials of catching the heavy ball with arm 1. The arm with which subjects started (i.e., arm 1) was counterbalanced; five subjects started with the right arm and four subjects started with the left arm.

In experiment 2, we tested intra-limb generalization. Subjects caught balls in either the bent or straight position, always with the right arm. Again, subjects completed a baseline phase, an adapta-

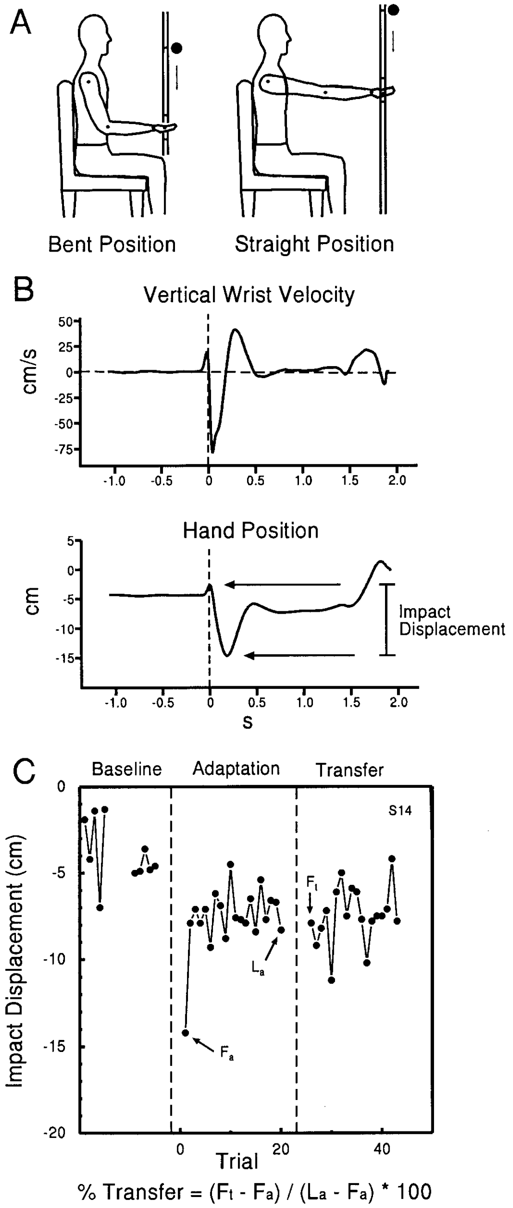


**Fig. 1** **a** Experimental setup showing bent and straight arm configurations. The ball was dropped from 40 cm above the center of the window. **b** A vertical wrist velocity trace (*top*) and a hand position trace (*bottom*) from a single trial from a typical subject demonstrating the selection of impact and the calculation of impact displacement. The trial is aligned on impact, marked by the *dashed vertical line*. **c** Calculation of percentage transfer. Impact displacement values are plotted as a function of trial from a typical subject. Trials are separated into the baseline, adaptation, and transfer phases. Specific trials of interest are indicated by *arrows*: $F_a$ is the first trial in the adaptation phase, $L_a$ is the last trial in the adaptation phase, and $F_t$ is the first trial in the transfer phase

tion phase, and a transfer phase. The baseline phase consisted of 8–12 trials of catching the light ball, first with the arm in either the bent or straight position (position 1) and then with the arm in the other position (position 2). The adaptation phase consisted of 18–22 trials of catching the heavy ball with the arm in position 2. The transfer phase consisted of 18–22 trials of catching the heavy ball with the arm in position 1. The position in which subjects started (i.e., position 1) was counterbalanced; three subjects started with the arm bent and five subjects started with the arm straight.

Prior to testing in both experiments, subjects were shown the two balls and were told which color was the light ball and which color was heavy. They were not told the precise weight nor were they allowed to feel the balls prior to testing. Subjects were told that they would begin by catching the light ball and were informed prior to switches in ball weight. They were also told that they would be asked to switch arms (experiment 1) or arm positions (experiment 2) periodically throughout the session. Subjects were instructed to begin each trial with the hand in the middle of the window. All subjects received 1–3 practice trials of catching the light ball before recording began. Feedback was given after every trial regarding whether they were successful in maintaining the hand within the window. All subjects received rest breaks approximately every seven trials to avoid fatigue.

## Data collection

The positions of the catching arm and the spatial window were recorded in three dimensions using the Optotrak System (Northern Digital, Waterloo, Ont.). Four infrared light-emitting diodes (IREDs) were placed on the arm to mark the position of the hand (second digit, metacarpophalangeal joint), wrist (styloid process of the radius), elbow (lateral epicondyle of the humerus) and shoulder (lateral head of the humerus). Three additional IREDs were placed on the vertical pole next to the catching arm to indicate the locations of the top and bottom of the window and the point from which the ball was dropped (Fig. 1a). Position data were collected at 100 Hz.

## Data analysis

Kinematic data were low-pass filtered at 10 Hz. We used Optotrak software to calculate marker positions, velocities, and joint angles. Custom software was used for the following analyses. For each trial, we determined the time of impact (the time of initial ball contact with the hand). Impact was chosen as the time when, after the ball was released, the vertical wrist velocity crossed the zero line (Lang and Bastian 1999; Fig. 1b). All trials were aligned on impact. We next calculated a value for impact displacement for each trial. Impact displacement was defined as the vertical distance traveled by the hand from the time of impact to the time of the first reversal in the direction of the hand path (Fig. 1b). Impact displacement values were plotted as a function of trial for each subject.

We used an exponential decay function to describe the impact displacement values as a function of trial for each subject during the adaptation phase. The decay constant from the exponential function represents the number of catches it would take to obtain $(1 - e^{-1})$ or approximately 63.2% of the total adaptation and has been widely used as a measure of the rate of adaptation (Deuschl et al. 1996; Martin et al. 1996a; Lang and Bastian 1999). Exponential functions were fit using CoStat software (CoHort Software, Berkeley, Calif.).

We also calculated a percentage transfer value for each subject to quantify the extent to which the adaptation generalized to the second condition; i.e., the second arm in experiment 1 or the second arm position in experiment 2. Percentage transfer was determined by:

$$\text{Percentage Transfer} = \left[\frac{(F_t - F_a)}{(L_a - F_a)}\right] \cdot 100 \tag{1}$$

where $F_t$ is the impact displacement from the first trial of the transfer phase, $F_a$ is the impact displacement from the first trial of the adaptation phase, and $L_a$ is the impact displacement from the last trial of the adaptation phase (adapted from Schmidt 1988). Figure 1c illustrates the method for calculating percentage transfer for a typical subject. Note that percentage transfer can exceed 100% if $F_t$ is less than $L_a$; that is, if the impact displacement on

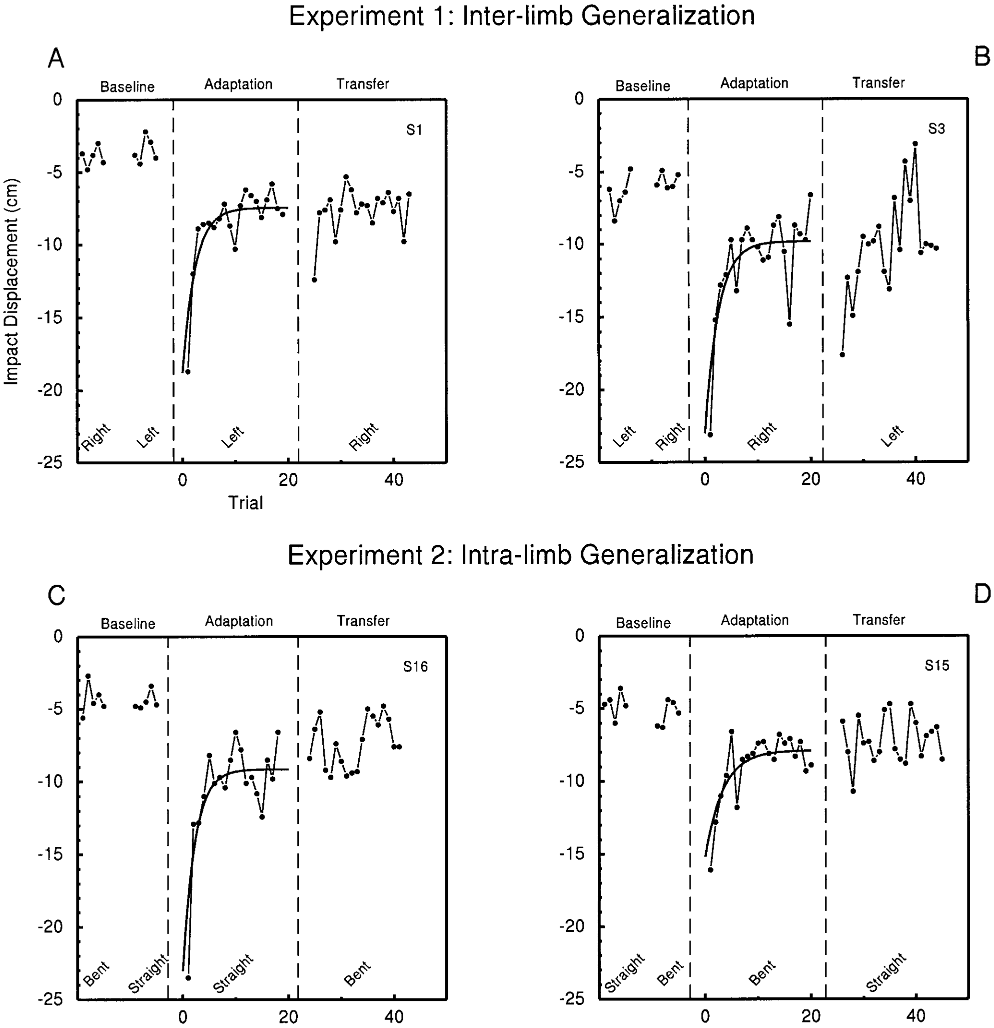


**Fig. 2a–d** Impact displacement values plotted as a function of trial from four representative subjects. Trials from the adaptation and transfer phases are shown in full, with the last five trials of the baseline phase for each arm (experiment 1) or each position (experiment 2) included for comparison. *Dashed vertical lines* separate the phases. Negative impact displacement values represent downward displacement from the resting position of the hand. The *curved line* in each adaptation phase represents the exponential fit from which the adaptation rates were determined. **a** Subject S1 (inter-limb experiment), who performed the adaptation phase with the left hand and the transfer phase with the right. **b** Subject S3 (inter-limb experiment), who performed the adaptation phase with the right hand and the transfer phase with the left. **c** Subject S16 (intra-limb experiment), who performed the adaptation phase in the straight position and the transfer phase in the bent position. **d** Subject S15 (intra-limb experiment), who performed the adaptation phase in the bent position and the transfer phase in the straight position

the first transfer trial is smaller than on the last adaptation trial. In the few cases (4 of 17) where transfer was more than 100%, we found that the hand remained within the window (e.g., did not rise above the top of the window) on the first transfer trial.

Finally, to quantify the type of strategy used to achieve the adaptation, we calculated the change in angle at the shoulder, elbow, and wrist joints that occurred between the time of impact and the first reversal in the direction of the hand path.

Prior to the main analysis, we used two separate ANOVAs to determine whether the starting arm (left or right) or arm configuration (bent or straight) caused differences in (1) the adaptation rate or (2) the impact displacement magnitude for the last baseline trial, the first adaptation trial, the last adaptation trial, the first transfer trial, and the last transfer trial. We found no differences between subjects who started with the right versus left arm, nor between subjects that started with a bent versus straight arm ($p > 0.05$). Therefore, the subsequent analyses were conducted using pooled data from each experiment.

Our main analysis was done to test whether the adaptation and subsequent transfer was similar between arms (experiment 1) versus within an arm (experiment 2). Student's $t$-tests were used to compare the adaptation rates and percentage transfer values between experiments 1 and 2. Repeated-measures ANOVA was used to compare impact displacement values between experiments 1 and 2 for the following selected trials: the last baseline trial, the first adaptation trial, the last adaptation trial, the first transfer trial, and the last transfer trial. When the ANOVA yielded a significant result, subsequent post hoc analyses were conducted using Tukey's honest significant different test. Statistica software was used for all statistical analyses (StatSoft, Tulsa, Okla.), with the criterion for significance set at $p < 0.05$.

## Results

All subjects adapted quickly to the changed ball weight. There were no differences in adaptation rates ($p > 0.05$) for subjects in experiment 1 (2.03 ± 0.11) versus experiment 2 (2.07 ± 0.25). These values were also similar to those found in control subjects from a previous study (Lang and Bastian 1999). All subjects performed better (i.e., had smaller impact displacement values) on the first trial of the transfer phase than they did on the first trial of the adaptation phase. However, subjects in experiment 1 (inter-limb generalization) did not show complete generalization, while subjects in experiment 2 (intra-limb generalization) showed nearly complete generalization.

Figure 2 shows impact displacement values per trial for four representative subjects. Data from two subjects who participated in experiment 1 (inter-limb generalization) are shown in Fig. 2a, b. Subject S1 (Fig. 2a) performed the adaptation phase with the left arm and the transfer phase with the right. Subject S3 (Fig. 2b) per-

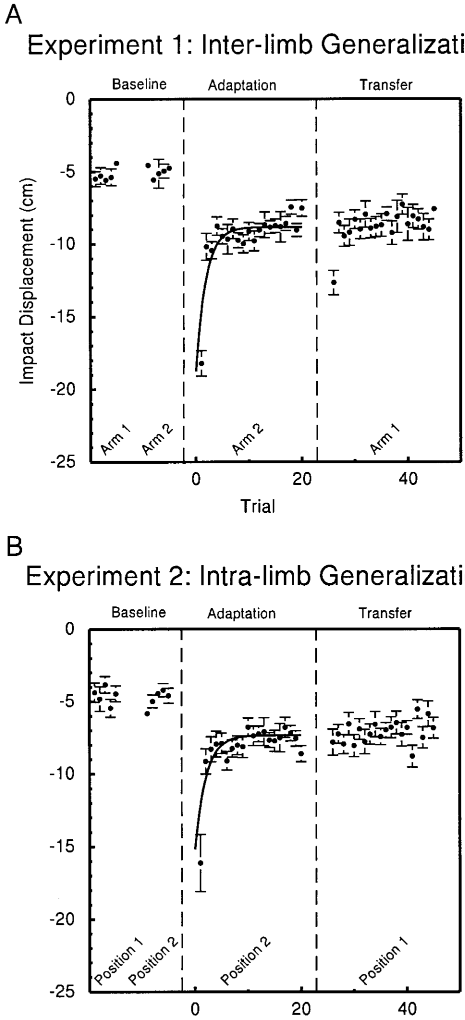


**Fig. 3** **a** Group impact displacement values (means ± 1 SE) from subjects in experiment 1 (inter-limb). **b** Group impact displacement values (means ± 1 SE) from subjects in experiment 2 (intra-limb)

**Table 1** Group impact displacement values (mean ± 1 SE, in centimeters) from selected trials for all subjects in experiments 1 and 2. The last baseline trial refers to the final baseline trial in the second condition (second arm or second arm position)

| Trial | Inter-limb generalization | Intra-limb generalization | Significance |
|---|---|---|---|
| Last baseline | –4.76 ± 0.2 | –4.59 ± 0.6 | $p = 0.78$ |
| First adaptation | –18.20 ± 0.9 | –16.11 ± 1.8 | $p = 0.31$ |
| Last adaptation | –7.51 ± 0.6 | –8.15 ± 0.6 | $p = 0.46$ |
| First transfer | –12.67 ± 0.8 | –7.80 ± 0.9 | $p = 0.001$* |
| Last transfer | –8.11 ± 0.4 | –6.82 ± 0.8 | $p = 0.16$ |

*Statistically significant difference in the post hoc analysis

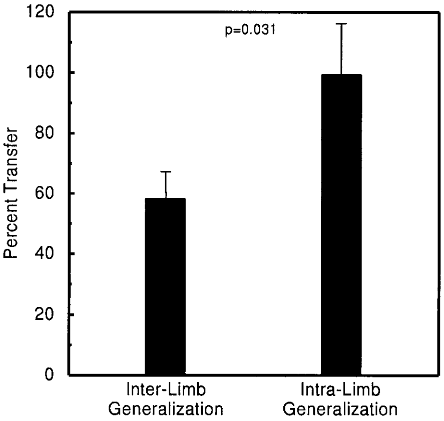


**Fig. 4** Group percentage transfer values (means ± 1 SE) for subjects in experiment 1 (inter-limb) and experiment 2 (intra-limb). See Fig. 1c for an illustration of the method used to calculate percentage transfer

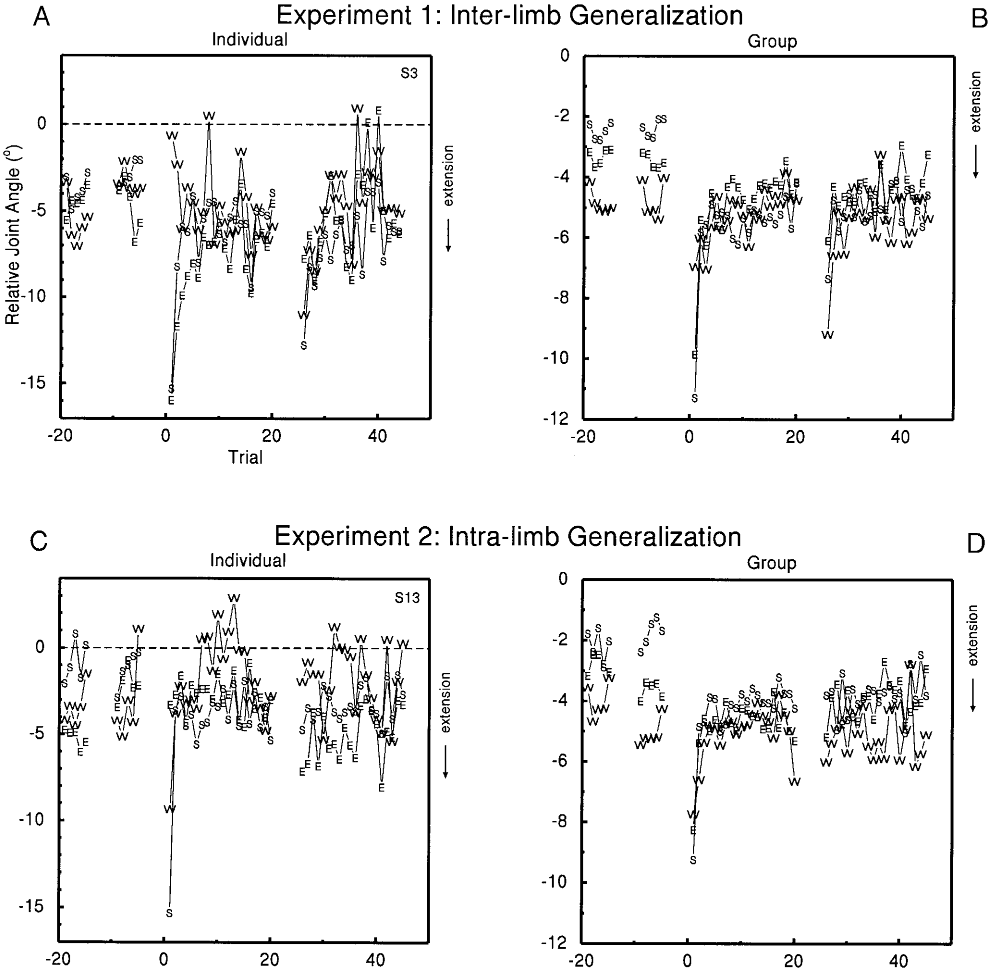
formed the adaptation phase with the right arm and the transfer phase with the left. Neither subject was able to catch the ball in the window on the first adaptation trial, but both were successful in the latter portions of the adaptation phase. Although both subjects had smaller impact displacements on the first trial of the transfer phase than during the first trial of the adaptation phase, they were nevertheless still unsuccessful in catching the ball within the 10-cm window on the first trial of the transfer phase.

Data from two subjects who participated in experiment 2 (intra-limb generalization) are shown in Fig. 2c, d. Subject S16 (Fig. 2c) performed the adaptation phase with the arm in the straight position and the transfer phase with the arm in the bent position. Subject S15 (Fig. 2d) performed the adaptation phase with the arm in the bent position and the transfer phase with the arm in the straight position. As with the subjects in experiment 1, neither subject was able to catch the ball in the window on the first adaptation trial, but both were successful in the latter portions of the adaptation phase. In contrast to the performance of subjects from experiment 1, these subjects were able to catch the heavy ball in the window on the first trial in the transfer phase. That is, they required no practice in the second arm configuration to successfully perform the task.

Figure 3 shows averaged impact displacement values for all subjects in experiments 1 and 2 plotted versus trial (Fig. 3a, b). On the first adaptation trial, neither group was able to catch the ball in the window, but both groups then adapted quickly. On the first transfer trial, both groups had smaller impact displacements, but only subjects in experiment 2 (intra-limb generalization; Fig. 3b) were successful on the first trial. Later trials in the transfer phase were similar to later trials in the adaptation phase in both groups.

Table 1 provides group impact displacement values for selected trials for all subjects in experiments 1 and 2. Repeated-measures ANOVA indicated a difference between subjects in experiment 1 and experiment 2. Subsequent post hoc analysis revealed a significant difference in impact displacement values for the first transfer trial ($p = 0.001$). Impact displacement was significantly smaller for subjects in the intra-limb generalization group compared with subjects in the inter-limb generalization group. The percentage transfer values also reflected the difference between the two groups (Fig. 4). Subjects

**Fig. 5a–d** Relative change in joint angles plotted versus trial. The change in joint angles was calculated between the time of impact and the first reversal in the direction of the hand path. Negative values represent joint movements in the direction of extension. Error bars have been removed for clarity; the variability both between and within subjects tended to be very large (*S* shoulder, *E* elbow, *W* wrist). **a** Subject S3 in experiment 1 (inter-limb). **b** Averaged data for all subjects in experiment 1. **c** Subject S13 in experiment 2 (intra-limb). **d** Averaged data for all subjects in experiment 2



participating in experiment 1 had a significantly smaller percentage transfer value (58 ± 9.09%) than subjects participating in experiment 2 (100 ± 15.80%, $p = 0.031$). Although both groups appeared to benefit from the prior experience of the adaptation phase, subjects who were asked to generalize across arms (experiment 1) were less successful in catching the heavy ball in the window on the first attempt compared with subjects who were asked to generalize within an arm (experiment 2).

Figure 5 shows the change in joint angles at the shoulder, elbow, and wrist during the period of time between impact and the first reversal in the direction of the hand path. Data from an individual who participated in experiment 1 (inter-limb generalization) and averaged data for all subjects in experiment 1 are shown in Fig. 5a, b, respectively. Data from an individual who participated in experiment 2 (intra-limb generalization) and averaged data for all subjects in experiment 2 are shown in Fig. 5c, d. Examination of these joint angles revealed two interesting findings. First, the adaptation was never isolated to a single joint. Every subject demonstrated changes in at least two, and often times three, joints during the adaptation phase. Second, the magnitude of each joint's displacement varied from trial to trial. A subject would often catch the ball using different patterns of joint movement on different trials. Thus, what appeared to be adapted was a combination, or sum, of joint displacements.

## Discussion

We have found that healthy people are capable of both inter- and intra-limb generalization of adaptive control of ball catching. Thus, the CNS has the capacity to use sensory information gathered during previous experiences in order to partially predict the necessary motor output to correctly perform the same task in a novel context. Other studies have shown generalization in a variety of upper-extremity tasks (Gordon et al. 1994; Shadmehr and Mussa-Ivaldi 1994; Dizio and Lackner 1995; Gandolfo et al. 1996; Conditt et al. 1997). Most, however, have not shown the same extent of generalization that we have demonstrated in either the inter- or intra-limb tasks. We hypothesize that the nature of the task at least in part predicts the greater extent of generalization seen during catching. Our catching task is relatively simple and is a skill with which most people are quite familiar. In addition, the subjects in this study were notified of the change in ball weight at the time of the switch. These factors undoubtedly contributed to the improved generalization. Other relatively simple, familiar tasks have also been shown to generalize to a large extent. Gordon et al. (1994) have shown that, when grasping and lifting small objects, weight-related information is transferred to the contralateral arm such that lifts with an unexposed arm reflect the force used in previous lifts with the other arm.

In the current study, we found that intra-limb generalization was complete, whereas inter-limb generalization was incomplete. The majority of subjects could catch the ball within the spatial window on the first trial after switching arm configurations (seven of nine subjects). In contrast, the majority of subjects *could not* catch the ball within the spatial window on the first trial after switching arms (seven of eight subjects). Because we see generalization between the limbs, we hypothesize that the generalization of ball catching relies on an internal representation of an external parameter of the task, which could then be utilized by either limb. We further propose that the external parameter stored in the CNS is the momentum of the ball (Lacquaniti and Maioli 1989; Lang and Bastian 2001). Lacquaniti and Maioli (1989) have shown that, during catching, subjects scale anticipatory muscle activity to the expected momentum of the ball, which depends on ball weight and also drop height. We have shown that anticipatory muscle activity is adjusted through practice when the ball momentum is changed (Lang and Bastian 1999). In addition, we found that prior information about the weight of the ball alone is insufficient to allow subjects to produce a successful catch on the first trial. Instead, subjects require explicit somatosensory information about the ball weight and drop height to produce a correct catch on the first trial (Lang and Bastian 2001). These results taken together suggest that partial inter-limb transfer is due to an internal representation of ball momentum, which can then be applied to movements generated by any effector. However, this information is insufficient to produce successful task performance on the first trial.

Prior exposure to the ball with the same arm in a different configuration typically produced successful catching performance on the first trial. This was the case even though the torque requirements for ball catching were dramatically altered with the arm in different configurations. For example, the torque requirements at the shoulder joint are more than doubled when switching from the bent to the straight arm configuration. For a typical subject catching the 770-g ball, the total torque required at the shoulder is approximately 7.5 Nm in the arm bent position versus approximately 16.2 Nm in the arm straight position (using standard anthropometric tables and assuming subject height 1.75 m, weight 712 N; Winter 1990). Therefore, the subjects could not have simply learned the torque requirements for the catch in a rote manner, a conclusion consistent with a study of reaching adaptation and generalization (Conditt et al. 1997). Rote memorization could only explain our findings in the intra-limb condition if the adaptation took place entirely at the wrist, since the wrist remained in essentially the same position in both the bent and straight arm configurations. However, the joint angular displacement values (see Fig. 5) indicate that the adaptation always occurred at multiple joints. Additionally, even within individuals, there was a large degree of trial-to-trial variability in which joint(s) were responsible for maintaining the hand in the window. Thus, the adaptation does not appear to be dependent on actions at specific joints but rather on some type of sum of the actions at all of the involved joints. It therefore seems likely that the information stored and used in the intra-limb generalization condition could not be joint specific. Instead, we speculate that subjects relied on an effector-specific internal sensorimotor representation of the required catching movement that can be modified by the position of the joints in the arm. Shadmehr and Moussavi (2000) have proposed recently that the joint position (e.g., shoulder angle) might act to globally modify a newly learned representation of arm dynamics adapted to a novel force field. We speculate that this type of mechanism could explain the near-perfect intra-limb transfer that we observed when subjects switched arm configurations, especially given the dramatic difference in torque requirements at the shoulder and elbow.

Based on previous work, it is possible that the site of storage for this type of representation is in the cerebellum. Individuals with cerebellar damage have an impaired ability to adapt to a novel ball weight during catching (Lang and Bastian 1999). Damage to the cerebellum also impairs the ability to accurately anticipate the necessary muscle activity for the catch even when given online sensory information (e.g., when subjects are allowed to drop the ball onto their own hand; Lang and Bastian 2001). In this condition, normal, healthy controls are able to successfully catch the ball in the window without any previous experience, suggesting that online information about the external (ball momentum, time of drop) and internal (limb configuration) parameters of the task combined with information about the dynamics of the catching arm (from the internal sensorimotor representation) is sufficient to generate the correct muscle activity even without any prior exposure to the task. This is in agreement with other studies that have shown that online sensory information is adequate to immediately and accurately predict a desired motor output (Johansson and Westling 1988; Hore et al. 1999). Given that individuals with cerebellar damage are unable to accurately predict the correct muscle activity even when provided with online information, it is possible that the cerebellum may be the storage location for this internal representation. Many other studies have also suggested that the cerebellum is a likely site for one or more internal models for limb movements (Kawato and Gomi 1992; Wolpert and Kawato 1998; Hore et al. 1999; Imamizu et al. 2000).

## Conclusions

We have demonstrated that normal healthy subjects show generalization of adaptation in a catching task. The generalization is incomplete across different arms and complete across different positions within the same arm. From these results, we speculate that the CNS utilizes different representations of task and limb parameters that can be adapted for use in novel conditions. One representation may contain information pertinent to specific external task parameters, such as the momentum of the ball, which could be utilized to improve catching performance by either arm. A second internal representation appears to be effector specific. We speculate that this sensorimotor representation may contain information about the dynamics of the arm-ball interaction which can be immediately modified by proprioceptive information about the arm configuration.

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