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
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 of 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-