Brain and Cognition 72 (2010) 385–393

Contents lists available at ScienceDirect

Brain and Cognition

journal homepage: www.elsevier.com/locate/b&c

Motor adaptation and manual transfer: Insight into the persistent nature of sensorimotor representations

Sharon Green [a], Lawrence E.M. Grierson [b], Adam Dubrowski [c], Heather Carnahan [d,*]

[a] Department of Kinesiology, University of Waterloo, Canada
[b] Toronto Rehabilitation Institute, Canada
[c] Lawrence Bloomberg Faculty of Nursing, University of Toronto, Canada
[d] Department of Occupational Science and Occupational Therapy, University of Toronto, Canada

ARTICLE INFO

Article history:
Accepted 20 November 2009
Available online 19 January 2010

Keywords:
Feedback
Feedforward
Sensorimotor memories
Motor adaptation
Illusions

ABSTRACT

It is well known that sensorimotor memories are built and updated through experience with objects. These representations are useful to anticipatory and feedforward control processes that preset grip and load forces during lifting. When individuals lift objects with qualities that are not congruent with their memory-derived expectations, feedback processes adjust motor plans to achieve successful lifts and contribute to the updating of the stored representations. The two experiments presented examine motor adaptation to an illusory size–weight lifting task, and the transfer of this motor adaptation to the unexposed hand. In Experiment 1, performers acquired motor adaptation with their right hand and transfer was measured on their left hand. In Experiment 2, adaptation was acquired with the left hand and transfer was measured on the right hand. In order to investigate the persistence of sensorimotor memories, these experiments measure adaptation, retention, and transfer after 15 min and 24 h delay periods. Both experiments confirm that experience with objects leads to adaptation of force scaling processes, that these adaptations transcend effector and are persistent. The results are discussed in terms favouring interpretations that describe motor adaptations to illusion as being centrally available.

1. Introduction

Gordon, Westling, Cole, and Johansson (1993) examined the force profiles individuals generated when they lifted common objects, as well as those produced when novel objects with unusually high (4.0 kg/L) or more common (1.2 kg/L) densities were lifted. The profiles evidenced that individuals scaled their fingertip forces efficiently to lift the common objects. That is, prior to the availability of any information regarding the object's weight, load forces – the forces tangential to the grasp surface (Johansson, 1996) – and their rates were unique to each common object on the first lift and remained consistent across 10 lifts. Interestingly, for the first lifts of the unusually dense objects individuals did not approach the object with a motor plan sufficient in force. Rather, these force profiles were similar to those produced when objects within the more common range of densities were lifted. However, even though lifters began with inadequate force outputs the resulting lifts were not unsuccessful; the profiles of which indicated that afferent feedback guided a probing strategy of slow stepwise force increases until the error was remedied (Gordon, Forssberg, Johansson, & Westling, 1991; Johansson & Westling, 1988). Furthermore, by the third lift, the initial motor plans were appropriately rescaled to the high density object and this adaptation was maintained 24 h later.

This work is among many instrumental studies that have highlighted the importance of experientially-gained sensorimotor memories to the formation of properly scaled motor plans (e.g., Flanagan, Bowman, & Johansson, 2006; Flanagan & Wing, 1997). Evidently, we estimate the mass of objects by evaluating their extrinsic size and shape characteristics against stored representations of similar objects. When these memories lead to erroneous force generation, feedback evaluation processes ensure the lift is successful and that memorial representations are updated. In this way, experience adapts anticipation progressively (Gordon et al., 1993; see also, Johansson & Westling, 1988; Westling & Johansson, 1984). And though, asymmetric manual performance findings (Taylor & Heilman, 1980), a high prevalence of ideomotor and limb-kinetic apraxias associated with left hemisphere damage (Frey, Funnel, Gerry, & Gazzaniga, 2005; Goldenberg, 2003; Haaland & Harrington, 1996; Haaland, Harrington, & Knight, 2000; Liepmann, 1920), and increased activations of the left hemisphere during ipsilateral arm movements as measured by motor evoked potentials (MEP) (Ziemann & Hallett, 2001) and functional

* Corresponding author. Address: Department of Occupational Science and Occupational Therapy, University of Toronto, 160-500 University Ave., Toronto, Ont., Canada M5G 1V7.
E-mail address: heather.carnahan@gmail.com (H. Carnahan).

0278-2626/$ - see front matter © 2009 Elsevier Inc. All rights reserved.
doi:10.1016/j.bandc.2009.11.006

magnetic resonance imaging (fMRI) (Johnson-Frey, Newman-Norlund, & Grafton, 2005; Kim et al., 1993) all lend support to models of motor dominance (Glickstein & Sperry, 1960; Goldenberg, 2003; Liepmann, 1920) that speculate that these representations are stored with a bias to use by the right side effectors (see also, Carmon, 1971; Criscimagna-Hemminger, Donchin, Gazzaniga, & Shadmehr, 2003; Dee, Benton, & Van Allen, 1970; Geschwind & Kaplan, 1962; Malfait & Ostry, 2004; Wyke, 1971), it is generally accepted that in healthy humans they are centrally-available and not effector-specific (cf. Sainburg & Kalakanis, 2000; Wang & Sainburg, 2003).

In contrast to the glut of studies that have investigated the hemispheric locale and effector-specificity of sensorimotor memory formation and storage, there is a relative dearth of research highlighting the temporal features of these representations. However, recent work from Chang, Flanagan, and Goodale (2008) reported that with a 10 s delay between lifts, motor adaptations to the size–weight illusion could be successfully transferred from the left hand to the right hand. The size–weight illusion is a robust phenomenon in which the lifting of two equally-weighted objects of differing size is accompanied by the consistent perception that the smaller object is heavier. Although hypotheses explaining the mechanisms responsible for the illusion vary from disparities in the lift's expected and actual sensory feedback (Ellis & Lederman, 1993; Gordon et al., 1991; Flanagan & Beltzner, 2000; see also von Holst, 1954) to cognitive-perceptual phenomenon that use this difference to rationalize the percept that the small object is heavier (Mon-Williams & Murray, 2000), it is generally agreed that the phenomenon must have some foundation in the lifters' experientially acquired memories of object heaviness (Charpentier, 1891; Murray, Ellis, Bandomir, & Ross, 1999). Importantly, there is compelling evidence that indicates that when dealing with the size–weight illusion the sensorimotor and cognitive-perceptual systems operate independently of each other (e.g., Flanagan & Beltzner, 2000; Grandy & Westwood, 2006). That is, experience with size–weight illusion objects leads forces to adapt to the appropriate mass of the objects, while the misperceptions of relative mass are maintained; a dissociation that persists at least 1 day later (Flanagan, King, Wolpert, & Johansson, 2001). In addition to confirming the central availability of acquired sensorimotor memories, the delayed transfer effects from Chang et al. (2008) study are particularly interesting insofar that they show that the accessibility of these representations has some temporal resiliency.

In order to extend the work of Chang et al. (2008), the current study used two transfer-of-training experiments to examine the extent that adaptation to erroneous force generation persisted when transferred from one hand to the other (Ammons, 1958; Ammons & Ammons, 1951; Ewert, 1926; Hicks, 1974 Laszlo, Baguley, & Bairstow, 1970; Parlow & Kinsbourne, 1989). The transfer-of-training paradigm was chosen to ensure that the representations adapted through experience and accessed in transfer are indeed centrally available. In Experiment 1, right-handed individuals were exposed to size–weight illusion objects with their dominant hand and retention and transfer of motor adaptation were measured on their right and left hand respectively, after 15 min and 24 h delay periods. Experiment 2 was designed similarly, however in this case, right-handed individuals acquired adaptation with their non-dominant hand and retention and transfer were measured on their left and right hands after the same delays. We hypothesize that, in both experiments, the performers will acquire appropriate sensorimotor representations for the lifted object during their initial phase of exposure to the illusion. We expect that this will be evidenced by efficiently scaled lift forces measured during the immediate retention testing. Furthermore, the presence or absence of appropriately scaled lift forces during the 15 min and 24 h retention-and-transfer tests will offer some insight into the temporal persistence and central availability of these representations. Lastly, any differential pattern of results yielded from Experiments 1 and 2 may contribute to arguments concerning the nature of hand dominance as well as the effector-specificity and hemispheric seat of sensorimotor representations.

2. Experiment 1

In Experiment 1 the size–weight illusion was used to test whether an adaptation to the illusion is retained by the right hand after 15 min and 24 h delays and if after these intervals, the adaptation is transferable to the left hand.

2.1. Method

2.1.1. Participants

Twelve naïve and healthy, right-handed University undergraduates (five males, seven females, mean age = 23.8 years) participated in the experiment. Handedness was determined by a modified version of Oldfield's (1971) Handedness Questionnaire and potential participants were excluded from participation if their laterality index was below 80.00 (5th right decile). All participants reported normal or corrected-to-normal vision. Informed consent was given prior to the initiation of testing as per the requirements of the local office of research ethics.

2.1.2. Apparatus

Participants grasped a six-axis force–torque sensor (Nano F/T transducer; ATI Industrial Automation, Garner, NC) with flat polyethylene plastic cylindrical ends attached to each grasping surface. The cylinder had a diameter of 3.5 cm and a length of 5.5 cm and was mounted onto one of two (large or small) aluminum objects each with an identical mass (384 g). The large object had a volume of 137.18 cm^3 (9.5 cm × 3.8 cm × 3.8 cm) while the small object had a volume of 54.87 cm^3 (3.8 cm × 3.8 cm × 3.8 cm). When mounted to either of the aluminum metal objects, the center of the grasping surface was located 8.5 cm above the tabletop. The total mass of the apparatus was 454 g (Fig. 1).

2.1.3. Procedure

2.1.3.1. Motor task. There were two-testing sessions. The first session included an acquisition phase and a 15 min retention-transfer test. The second session involved a 24-h retention-transfer test. The acquisition phase consisted of alternating right-handed lifts between the large and small objects. To begin participants sat at a table and rested their right thumb and index finger on the tabletop at a starting position marked 15 cm away from the mounted

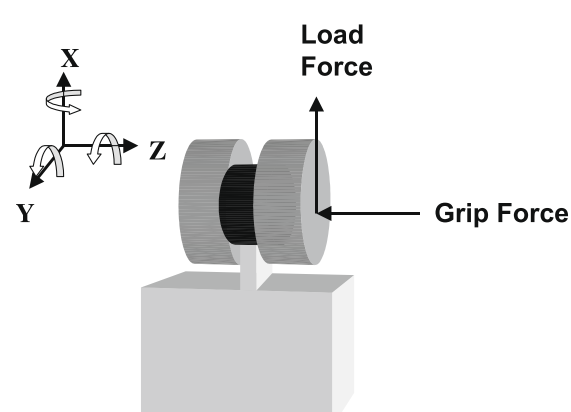

Fig. 1. Schematic representation of forces and torques.