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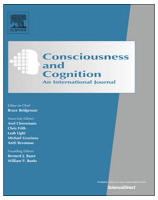

Explicit and implicit components of visuo-motor adaptation: An analysis of individual differences

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ABSTRACT

Adaptation to visuo-motor rotations embraces implicit and explicit components. We contrast this two-component model with a three-component model by means of an individual-differences approach. Adaptive changes were tested under four conditions: (1) closed-loop test, presence of the rotation cued (initial adaptive shift), (2) open-loop test, presence of the rotation cued (adaptive shift), (3) open-loop test, absence of the rotation cued (after-effect), (4) test of explicit knowledge (explicit shift). After-effects and explicit shifts were uncorrelated. After regression on after-effects and explicit shifts, the residuals of the initial adaptive shifts and the adaptive shifts remained correlated, suggesting an additional implicit component of adaptation found only in the cued presence of the visuo-motor rotation. The two implicit components are consistent with the distinction between a change of the body schema giving rise to after-effects, and the development of an internal model of a tool that is applied only when the transformation is present.

1. Introduction

During their lifetime, humans experience a vast range of relations between their muscular activity and the visual consequences thereof. Such variations result from bodily growth and age-related changes of muscular function, from muscle fatigue, from variations in visuo-motor mapping as they are introduced by optical devices such as glasses, and perhaps most frequently from the use of tools and the manipulation of objects with different masses. The changes occur on different time scales, and adaptation mirrors the different scales (cf. Körding, Tenenbaum, & Shadmehr, 2007; Smith, Ghazizadeh, & Shadmehr, 2006). However, adaptation is not a unitary process, but different processes contribute distinct components even for simple experimental changes of visuo-motor relations as in the classic prismatic displacement (cf. Welch, 1978, chapter 3, for an overview) or the more recent visuo-motor rotation paradigm (cf. Saijo & Gomi, 2010). In the present study we analyse individual differences in different tests of adaptive change in response to a visuo-motor rotation to shed new light on the processes involved.

1.1. Components of adaptation to visuo-motor rotation

Since the seminal study of Cunningham (1989), adaptation to visuo-motor rotation has become a major paradigm for the study of visuo-motor plasticity. Typically movements are performed in a horizontal plane, and visual feedback is provided by

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a cursor presented on a monitor. The visual feedback is rotated relative to the direction of hand movement, generally by 30° or more. In many studies the monitor is placed in front of the participants so that movements of hand and cursor are in different places and planes (e.g., Krakauer, Pine, Ghilardi, & Ghez, 2000). In some studies the monitor is viewed in a mirror and placed in such a way that the cursor appears in the same plane in which the hand is moved (e.g., Abeele & Bock, 2003). Movements are mostly performed from a central start position to targets in equidistant directions. Visual feedback can be provided during each movement or only after its end (e.g., Heuer & Hegele, 2008a; Nikooyan & Ahmed, in press). Movements can be slow and accurately reach the target (e.g., Hegele & Heuer, 2010a,c), or they can be rapid reversal movements that can hardly be corrected based on visual feedback (e.g., Bock, 2005). The main finding is robust across the procedural variations: in the course of practice the initial direction of hand movements is gradually shifted away from the target direction to the adapted direction that partially or fully compensates the visuo-motor rotation.

The adaptive changes observed during practice can result from changes of both feedback and feedforward control. Changes of feedforward control can be isolated by way of open-loop tests in which no visual feedback is available. An alternative way to assess changes of feedforward control even in the presence of visual feedback is to measure the direction of a movement early in its course at a time at which movements cannot yet be affected by feedback-based corrections. When an open-loop test is used, the observed change of movement direction relative to a pre-test before the exposure to the novel visuo-motor rotation is often called an after-effect. However, it is crucial to distinguish two types of visual open-loop tests. In the one type of test, participants know that the visuo-motor rotation is on, even though there is no visual feedback. In the other type of test they know that the visuo-motor rotation is no longer in effect. Only the changes in the latter kind of test we call after-effects, but those in the first kind of test we call adaptive shifts (cf. Heuer & Hegele, 2008b).

The main difference between adaptive shifts and after-effects is that only the former, but not the latter, should be affected by deliberate strategic corrections. We conceive of strategic corrections as conscious and intentional shifts of the effective target away from the target actually presented, based on explicit knowledge of the visuo-motor rotation. Because in the after-effect test participants know about the absence of the visuo-motor rotation, they have no reason to make use of their explicit knowledge. In contrast, explicit knowledge should contribute to adaptive shifts which are measured in the cued presence of the rotation. In only a few studies explicit knowledge or strategic corrections were also assessed separately (e.g., Bock, 2005; Heuer & Hegele, 2008b; Taylor, Krakauer, & Ivry, 2014).

From the above considerations two components of adaptive changes of feedforward control can be distinguished, namely deliberate strategic corrections based on explicit knowledge and implicit adaptive changes. In the present study we assess these components in four different tests. The first one is a test of explicit knowledge of the visuo-motor rotation, and the second one is a visual open-loop test in which the absence of the visuo-motor rotation is cued. These two tests measure explicit shifts and after-effects, respectively, and they should tap explicit knowledge and implicit changes separately. The third test is a visual open-loop test in which the presence of the visuo-motor rotation is cued. The adaptive shifts measured in this test should be affected both by explicit knowledge and implicit adaptive changes. Finally, the fourth test is a visual closed-loop test. In this test we assess adaptive changes early in the course of each movement before feedback-based corrections can produce dominant effects. These initial adaptive shifts again should be affected both by explicit knowledge and implicit changes.

The distinction between implicit and explicit (or strategic) components of visuo-motor adaptation is a fundamental one, although the specific definitions and denominations may vary (cf. Redding, Rossetti, & Wallace, 2005). The repeatedly observed additivity of the components suggests that they are functionally independent (Mazzoni & Krakauer, 2006; Sülzenbrück & Heuer, 2009; Taylor & Ivry, 2011). For example, strategic corrections can be instructed to fully compensate the visuo-motor rotation. In spite of the correct movements, the implicit component of adaptation is added to the strategic correction in the course of practice so that the rotation becomes over-compensated (Mazzoni & Krakauer, 2006). However, in spite of their functional independence the two components can be interrelated via the joint outcome they produce. Thus, after sufficiently extended practice the errors of over-compensation can be reduced again, suggesting an adjustment of the strategic corrections (Rand & Rentsch, in press; Taylor & Ivry, 2011).

Studies of adaptation to visuo-motor rotation and to other visuo-motor transformations have revealed several distinguishing features of the explicit and implicit components of adaptation. For example, explicit components generalize across target directions, whereas implicit components are restricted to a limited asymmetric range around the practiced target direction (Heuer & Hegele, 2008b, 2011; Izawa, Criscimagna-Hemminger, & Shadmehr, 2012; Krakauer et al., 2000). Similarly, explicit components generalize across a wide range of the workspace, whereas generalization of implicit components is more limited (Heuer & Hegele, 2011). Under certain conditions only explicit components allow dual adaptation to rotations in opposite directions, whereas implicit components cancel each other (Hegele & Heuer, 2010b). Explicit components suffer at older adult age, whereas implicit components are robust – this contrast has been supported by several studies with different experimental protocols (e. g., Bock, 2005; Bock & Girgenrath, 2006; Buch, Young, & Contreras-Vidal, 2003; Hegele & Heuer, 2010a,b; Heuer & Hegele, 2008b; McNay & Willingham, 1998). Finally, implicit components, but not explicit ones, depend on intact cerebellar functions (Taylor, Klemfuss, & Ivry, 2010).

Explicit and implicit components of adaptation may themselves be heterogeneous. Consider the implicit adaptive changes. These have been described, for example, as realignment (Redding et al., 2005) or in terms of an internal model of the transformation (Wolpert & Kawato, 1998). In part these changes may also consist of changes of position sense, in particular of a re-calibration of proprioception. The extent of such re-calibration seems to vary with rather unknown conditions (cf. Cressman & Henriques, 2009, 2010; Cressman, Salomonczyk, & Henriques, 2010; Hegele & Heuer, 2010b; Wong &