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Properties of intermodal transfer after dual visuo- and auditory-motor adaptation

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ABSTRACT

Previous work documented that sensorimotor adaptation transfers between sensory modalities: When subjects adapt with one arm to a visuomotor distortion while responding to visual targets, they also appear to be adapted when they are subsequently tested with auditory targets. Vice versa, when they adapt to an auditory-motor distortion while pointing to auditory targets, they appear to be adapted when they are subsequently tested with visual targets. Therefore, it was concluded that visuomotor as well as auditory-motor adaptation use the same adaptation mechanism. Furthermore, it has been proposed that sensory information from the trained modality is weighted larger than sensory information from an untrained one, because transfer between sensory modalities is incomplete. The present study tested these hypotheses for dual arm adaptation. One arm adapted to an auditory-motor distortion and the other either to an opposite directed auditory-motor or visuomotor distortion. We found that both arms adapted significantly. However, compared to reference data on single arm adaptation, adaptation in the dominant arm was reduced indicating interference from the non-dominant to the dominant arm. We further found that arm-specific aftereffects of adaptation, which reflect recalibration of sensorimotor transformation rules, were stronger or equally strong when targets were presented in the previously adapted compared to the non-adapted sensory modality, even when one arm adapted visually and the other auditorily. The findings are discussed with respect to a recently published schematic model on sensorimotor adaptation.

1. Introduction

A key-feature of the sensorimotor system is its flexibility: humans can adapt their eye, arm and leg movements to a variety of sensorimotor discordances. When, for example, visual feedback about arm position is rotated clockwise by 30 degrees, participants see their arm moving 30 degrees clockwise from the intended target; this error is adaptively reduced with extended practice, and participants see their arm moving directly towards the target again. When the feedback is turned back and corresponds to the movement again, movement directions deviate to the opposite direction compared to the previous rotation, which is interpreted as aftereffect or 'true adaptation' (Weiner, Hallett, & Funkenstein, 1983).

One of the first researchers, who investigated the locus of adaptive changes, was Harris (1963). He found that visuomotor adaptation transfers well from the visuomotor to the auditory-motor system (intermodal transfer), but marginally from the adapted to the non-adapted hand. Up to now, many studies have replicated or modified his paradigm. Their results were equivocal. Several studies observed a transfer of sensorimotor adaptation from the practiced to the unpracticed arm: subjects who adapted to a

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visuomotor discordance while using one arm subsequently remained adapted even when using their other arm (Cunningham & Welch, 1994; Fernández-Ruiz, Diaz, Moreno-Briseño, Campos-Romo, & Ojeda, 2006; Imamizu & Shimojo, 1995). However, other authors found little or no interlimb transfer (Abeele & Bock, 2001; Bock, 1992; Harris, 1963; Kitazawa, Kimura, & Takanori, 1997; Mikaelian, 1972), or reported that this transfer is contingent on task constraints such as continuous versus terminal vision of the arm (Cohen, 1967), gradual versus abrupt introduction of the distortion (Malfait & Ostry, 2004; Michel, Pisella, Prablanc, Rode, & Rossetti, 2007), geometry of the distortion (Tuan & Jones, 1997; van den Dobbelsteen, Brenner, & Smeets, 2003), distribution of practice (Taub & Goldberg, 1973), hand dominance (Sainburg & Wang, 2002), workspace location (Wang & Sainburg, 2006), head mobility (Hamilton, 1964), and attentional focus (Bedford, 2007; Canon, 1971).

A complementary group of studies investigated intermodal transfer: subjects adapted to a visuomotor discordance while responding to targets of one sensory modality, and were subsequently tested with targets of another modality. The outcome was again diverse: intermodal transfer was strong in some (Craske, 1966; Harris, 1963; Kagerer & Contreras-Vidal, 2009; Simani, McGuire, & Sabes, 2007), absent in another (Bernier, Gauthier, & Blouin, 2007), and depended on task constraints in yet other studies (Cohen, 1974; Michel et al., 2007; Mikaelian, 1974).

Another approach dealt with concurrent adaptation to two different distortions. Subjects were exposed to one distortion while using the right arm, and to the opposite distortion while using the left arm; distortions and arms alternated between successive trials, blocks of trials, or between the first and second half of the experiment. In either case, subjects adapted successfully with either arm to the respective distortion (Martin & Newman, 1980; Prablanc, Tzavaras, & Jeannerod, 1975), and they did so as quickly (Galea & Miall, 2006) and as completely as in unimanual adaptation (Bock, Worringham, & Thomas, 2005; Galea & Miall, 2006; Mikaelian & Malatesta, 1974). Another group of studies found that subjects can adapt even with a single arm to two opposing distortions; for this, each distortion must be cued by a different arm posture (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Ghahramani & Wolpert, 1997; Hwang, Donchin, Smith, & Shadmehr, 2003), workspace quadrant (Woolley, Tresilian, Carson, & Rick, 2007), gaze direction (Hay & Pick, 1966), head orientation (Seidler, Bloomberg, & Stelmach, 2001), verbal alert (Imamizu et al., 2007), acoustic signal (Kravitz, 1972), or visual information (Osu, Hirai, Yoshioca, & Kawato, 2004; Rao & Shadmehr, 2001; Wada et al., 2003).

A recent conceptual model accommodates for all these findings (Bock, 2013). It postulates the existence of multiple parallel sensorimotor pathways called "adaptive mechanisms", which are composed of special purpose modules. Some of these modules are directionally selective and regulate gradual adaptation of movement directions. The main features of this model are illustrated in Fig. 1. Dual adaptation is explained by adaptation of two mechanisms, which are linked to motor output by a context-dependent switch, whereby switch position represents a learned association between an adaptive mechanism and adaptation context. For example, when the right arm adapts to counterclockwise rotated feedback and the left arm to clockwise rotated feedback, the sensorimotor system learns to associate the right arm with one adaptive mechanism and the left arm with the second adaptive mechanisms (Bock & Schmitz, 2013). Furthermore, the black elements in Fig. 1 illustrate that effectors are weighted, whereby the trained effector is weighted larger than the untrained effector (Bock, 2013). Thus, strong intermanual transfer can be explained by a large weighting factor W5 and W6, whereas weak intermanual transfer is reflected by small values of W5 or W6.

Recently, Schmitz and Bock (2014) investigated the role of different input modalities for sensorimotor adaptation. They documented that following auditory-motor adaptation, aftereffects emerged not only with auditory, but also with visual targets. They further reported that aftereffects following auditory-motor adaptation were of similar magnitude as those following visuomotor adaptation if feedback was provided in a similar fashion, and that aftereffects in the trained sensory modality were larger than those in the untrained modality (Schmitz & Bock, 2014). In other words, visuomotor adaptation led to larger aftereffects with visual than with auditory targets, but the opposite was the case for auditory-motor adaptation. These findings led us to modify tenets of the conceptual model (Bock, 2013): as shown by the gray elements in Fig. 1, sensory information is weighted before entering the adaptive mechanisms; the weights are larger for sensory information from a trained than for an untrained sensory modality, but they don't depend on whether the information comes from the visual or the auditory modality (Schmitz & Bock, 2014). Thus according to Fig. 1, adaptation of the right hand to distorted visual feedback increases W1 and W5 compared to W2 and W6, respectively. Similarly, adaptation of both hands to opposite visual distortions increases W1 and W3, compared to W2 and W4, and also increases W5 or W6.

The present study tested the tenets of the model from Bock (2013) with a new set of experiments on dual adaptation. We hypothesized (hypothesis 1) that adaptation of two arms to opposite directed distortions does not depend on whether distortions are visually or auditory. Therefore, two groups of participants adapted with both arms to opposite directed distortions: Both groups pointed with the left arm to auditory targets and adapted to clockwise rotated auditory feedback. One of these groups (group *AA-dual*) pointed with the right arm to auditory targets and adapted to counterclockwise rotated auditory feedback, whereas the other group (group *VA-dual*) pointed with the right arm to visual targets and adapted to rotated visual feedback. To test the tenets of the model illustrated in Fig. 1, hypothesis 1 was further specified: Firstly (hypothesis 1a), one adaptive mechanism regulates adaptation of the left arm and a second adaptive mechanism adaptation of the right arm. This would become evident from decreasing performance errors in the adaptation-phases of both arms as well as significant aftereffects in each arm for the previously adapted modality. Accordingly, group *AA-dual* should reveal significant auditory-motor aftereffects in the left as well as the right arm, whereas group *VA-dual* should reveal auditory-motor aftereffects in the left and visuomotor aftereffects in the right arm. Furthermore, we predicted (hypothesis 1b) that alternating adaptation of both arms trains the context-dependent switch in Fig. 1 to connect to adaptive mechanism 1 when one left arm is used and to adaptive mechanism 2 when the other arm is used. This would be evident, when dual adaptation progresses with no signs of interference between arms as was the case for dual adaptation to *visuo*motor discordances (Bock & Schmitz, 2013; Bock et al., 2005; Galea & Miall, 2006; Prablanc et al., 1975); i.e.; neither performance during the adaptation-phases nor the aftereffects should be worse in groups *AA-dual* and *VA-dual* compared to groups of a reference study (Schmitz & Bock,