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Paradoxical adaptation of successful movements: The crucial role of internal error signals

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ABSTRACT

Visuo-motor adaptation has been classically studied using movements aimed at visual targets with visual feedback. In this type of experimental design, the respective roles of the different error signals cannot be fully disentangled. Here, we show that visuo-motor adaptation occurs despite the terminal success of the action and the compensation of the external error by a jump of the visual target. By using three grasping task conditions we manipulated the retinal error signal between the seen hand and the target (external error) and the conflict between the hand's visual reafference and either the proprioceptive or the efference copy signal (internal error), in order to estimate their respective roles in prism adaptation. In all conditions, subjects were asked to rapidly grasp an object. In the classical 'Prism' condition the object was stationary, which provided both external and internal errors. In the 'Prism & Jump' condition, at movement onset the object was suddenly displaced (jump) toward its virtual image location (visually displaced by the prism) which also corresponded to the location where the movement was planned to and executed through prisms. This jump therefore cancelled the external error (between the seen target and the seen hand), whereas the internal error (between the seen hand and the expected visual reafference of the hand, or between the seen hand and the hand felt by proprioception) was unchanged (because it is independent of the presence of the goal). In the 'Jump' condition, the movement was planned and executed without prismatic goggles and consequently with no internal error (no difference between where the hand visual reafference is expected to be and where it actually is), but the object was suddenly displaced at movement onset by a displacement equivalent to a prism shift which provided an external error. The 'Prism' and 'Prism & Jump' conditions exhibited similar aftereffects, whereas no aftereffect was observed in the 'Jump' condition. These results suggest that successful actions can be subjected to adaptation and that internal error is the only signal necessary to elicit true visuomotor adaptation characterized by context-independent generalization.

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1. Introduction

The aim of sensori-motor adaptation is to ensure successful adjustment of body and limbs interaction with the environment perceived through our senses. An example of the most elementary action-to-perception interaction is the capture of an object by the saccadic eye movement system while maintaining space constancy (Bridgeman, 1975, 1979; Bridgeman, 1995, 2010; Deubel, Bridgeman, & Schneider, 1998; Wurtz, 2008). When the accuracy of the saccadic response is artificially altered, the amplitude of the saccade is progressively adjusted to ensure a successful foveal capture of the object. Adaptation is obtained by progressively modifying the following responses after an error has been detected at the end of the saccade. Another major example of physical interaction with the environment is the action of reaching and grasping objects visually perceived through glasses. Two types of representations of visual space can be distinguished: a cognitive representation driving perception, and a sensorimotor representation that controls visually guiding behavior (Bridgeman, Lewis, Heit, & Nagle, 1979, 2000; Goodale et al., 1986; Goodale and Milner, 1992; Rossetti et al., 1998; Bridgeman and Huemer, 1998; Bridgeman et al., 2000; Pisella et al., 2000; Pisella and Mattingley, 2004). The adaptation of the sensorimotor representation allows motor commands adjustments to be processed in several ways. Adjustments can derive from two main sources of error signals: once a movement has been programmed and initiated, it can be controlled and adjusted during its execution based on reafferences (1) comparing seen hand and target locations ("external errors") or (2) comparing seen hand location with expected (derived from efference copy) hand location or/and proprioception ("internal errors"). These two internal and external sources of errors are present both during the movement (dynamic error signals) and at the end (static terminal error). While dynamic errors can be used for both on-line motor control and offline modification of subsequent motor planning, terminal errors are used off-line to optimize the planning of the next movement by discrete feedforward control (e.g. Bastian, 2008; Held and Freedman, 1963; Kornheiser, 1976; O'Shea et al., 2014; Redding, Rossetti, & Wallace, 2005; Welch, Bridgeman, Anand, & Browman, 1993; Weiner, Hallett, & Funkenstein, 1983). It is interesting to note that terminal error is considered as a source of adaptation for both eye and arm movement systems (Hopp and Fuchs, 2004; Inoue et al., 2015; Kitazawa, Kohno, & Uka, 1995; Magescas and Prablanc, 2006; McLaughlin, 1967; Pelisson, Alahyane, Panouilleres, & Tilikete, 2010).

Prismatic displacement of the visual field has been extensively used to study sensori-motor adaptation of the arm in the laboratory (Redding et al., 2005; Welch et al., 1993; Welch, 1986). Under prismatic laterally displaced vision, visuo-motor behavior is altered because movements are directed toward the virtual image of the visual goal. Then visuo-motor adaptation to the optical shift gradually develops across trials, and accuracy is gradually improved (for reviews Welch, 1974, 1986). However, true adaptation should be assessed by the existence of compensatory aftereffects, i.e. reaching errors in the opposite direction when prism glasses are removed (O'Shea et al., 2014; Redding et al., 2005). Indeed, instead of a "true adaptation" (Weiner et al., 1983), a context-dependent learning (such as pointing with left-right reversed visual feedback (Werner and Bock, 2010) can occur based on strategic feedforward control that will not affect the visuomotor behavior once prisms are removed. These two modes of prism compensation can dissociate in cerebellar patients who are specifically impaired for adaptation (Weiner et al., 1983), as is confirmed by brain stimulation interference (Panico, Sagliano, Nozzolillo, Trojano, & Rossetti, 2018). And they can be distinguished by specific kinematic markers as they affect either movement initiation or feedback control (O'Shea et al., 2014). In order to adapt, error signals can be used by the nervous system about the necessity to modify the automatic/spontaneous general sensori-motor correspondences. Obviously, in absence of error signal none of these mechanisms should be activated. True adaptation should be activated when internal and external errors are attributed to our own sensori-motor performance (prism, noncontact gravito-inertial field) whereas context-dependent learning should be activated when these errors are attributed to a specific external interface (such as a mouse, or manipulandum). We therefore postulate that internal error is more prone to elicit true adaptation than external error. In the present study, we implemented a paradigm in which external errors generated by prisms were cancelled by a fast computer-controlled target jump toward its virtual image. This allowed us to investigate whether performing successful actions (i.e. actions reaching successfully their goal from the first trial) in a distorted environment (through prisms) prevents the development of visuo-motor adaptation.

Visuo-motor adaptation has been classically studied with pointing movements aimed at visual targets. In order to make the final success of the action more compelling to the subject, we used overhand reach-to-grasp movements aimed to small objects in three experimental conditions (see Fig. 1). In a reference condition ('**Prism**' condition), subjects were instructed to grasp an object while wearing prism glasses. With prisms on, subject inappropriately planned movement towards the virtual location of the object, which led to a failure of the grasping action. In this condition, a classical visuo-motor adaptation is expected to develop based both on (static and dynamic) external and internal errors (see Table 1). In the crucial test condition ('**Prism & Jump**' condition), subjects wore the same prism glasses but the object was suddenly displaced (Jump) at movement onset onto the location of its virtual image, thus bringing the object to the intended hand location. The jump of the object therefore cancelled the external visual error as soon as the object displacement was completed (see Table 1). In this crucial condition, two predictions can be made. If the ultimate goal of sensori-motor adaptation is to ensure successful motor achievement, a null terminal feedback error should prevent sensori-motor plasticity. Verification of this prediction would confirm the preponderant role of external error signals in sensori-motor adaptation or learning. If, on the contrary, the adaptive mechanism aims at maintaining consistency between motor performance and predictive models of our actions, it would depend on the comparison between the intended movement and the actual movement performed, irrespective of the presence of the object, and a successful grasping of the object should not prevent adaptation. The argument here is that corollary discharge (or efference copy) provides predictive information that can be compared to actual visual reafferences. This comparison seems to be most effective when predictive and actual information are available nearly simultaneously (Held, Efstathiou, & Greene, 1966; Kitazawa et al., 1995), suggesting the implication of efference copy (the precursor of forward internal models) in adaptation (Bossom and Ommaya, 1968). The internal errors are present during and at the end of the movement. Thus, our second, alternative, prediction is that our 'Prism & Jump' condition will give rise to significant adaptation. If this prediction is verified, the