# Error correction and spatial generalization in human grasp control

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A R T I C L E   I N F O

A B S T R A C T

The visual processes that support grasp planning are often studied by analyzing averaged kinematics of repeated movements, as in the literature on grasping and visual illusions. However, by recalibrating visuomotor mappings, the sensorimotor system can adjust motor outputs without changing visual processing, which complicates the interpretation of averaged behavior. We developed a dynamic model of grasp planning and adaptation that can explain why some studies find decrements in illusion effects on grasping while others do not. In two experiments, we tested grasping in a standard three-phase adaptation paradigm and analyzed adaptation aftereffects on the maximum grip aperture as well as the error correction parameters estimated by our model. Experiment 1 demonstrated that the model accounts for adaptive responses to positive and negative visual size perturbations. Experiment 2 supported the novel hypothesis that visuomotor mappings for grasp planning can compensate for opposing size perturbations when these perturbations are experienced in separate regions of space. Our findings serve to illustrate how the surprising flexibility of grasp adaptation can hide (especially in session-wise averages) the true effects of visual perturbations on the visual processes that drive grasp planning.

## 1. Introduction

### 1.1. Visuomotor adaptation and session-wise averages

The control of goal-directed actions depends on finely tuned mappings between the visual, proprioceptive, and motor domains of the human sensorimotor system. Adaptation research is primarily concerned with understanding how these mappings change upon exposure to altered sensorimotor contingencies, like those produced by prism glasses, virtual reality environments, and force field manipulanda (Harris, 1963; Kornheiser, 1976; Cunningham, 1989; Ghahramani, Wolpert, and Jordan, 1996; Krakauer, Pine, Ghilardi, and Ghez, 2000; Shadmehr, Smith, and Krakauer, 2010). In a standard adaptation paradigm, the onset of a sensory perturbation initially harms performance, but practice under the new conditions leads to rapid improvement. Importantly, adaptation is only rarely accompanied by changes in the visual processes that estimate object properties for movement planning. Rather, the loci of adaptation are downstream mappings that transform the visual estimates into various motor coordinates. While the large majority of adaptation research focuses on reaching movements, a handful of studies have shown that the mappings supporting grasp planning also adapt when visual target sizes do not match the physical sizes felt at contact (Gentilucci, Daprati, Toni, Chieffi, and Saetti, 1995; Säfström and Edin, 2004, 2005, 2008; Weigelt and Bock,

2007; Coats, Bingham, and Mon-Williams, 2008).

Critically, given that motor behavior depends on visual information and the changing states of visuomotor mappings, averaging across multiple movements can produce results that conceal the effect of an applied sensory perturbation. However, session-wise averaging remains a standard practice in studies of visually guided action. In some cases, the averaged relationship between motor kinematics and physical target dimensions is interpreted as a direct reflection of visual processing for motor control. One example that illustrates why this can be problematic is the well-known finding that grasping movements are often more resistant to visual illusions than perceptual judgments (Aglioti, DeSouza, and Goodale, 1995; Ganel, Tanzer, and Goodale, 2008; Bruno and Franz, 2009). This finding is typically cited to support the claim that the visual system is divided into two functionally independent streams, following the proposal of Goodale and Milner (1992): vision-for-action (mediated by dorsal cortical regions) and vision-for-perception (mediated by ventral cortical regions).

The problem with this inference is that motor responses can rapidly adapt to visual perturbations while perceptual responses typically do not, due to obvious differences in their sensory feedback profiles. Thus, it may be the case that the dorsal and ventral visual streams differ not in their style of visual processing, but in their downstream connectivity with flexible, feedback-sensitive visuomotor mappings. Although connectivity with visuomotor mappings should correlate with the

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perception-action distinction proposed by Goodale and Milner (1992), this characterization of the dorsal stream abandons the strict dichotomy of perceptual and motoric processing in favor of a dynamic, multi-sensory model. Admittedly, visuomotor adaptation alone cannot explain all previously observed differences between perceptual and visuomotor responses, nor does it undermine all previous conclusions based on session-wise averages. Our overarching point is simply that it is necessary to properly account for the modulating influence of visuomotor adaptation when attempting to identify differences in the visual mechanisms that support perceptual and visuomotor functions.

### 1.2. Model of grasp planning and adaptation

Since the debate over the functional dissociation of vision-for-action and vision-for-perception is an active research domain that demands better accounting for adaptation effects, we focused on this literature in developing a mechanistic model of grasp planning and adaptation. Previous reviews of the illusions and grasping literature have indirectly suggested the potential importance of visuomotor adaptation by pointing out that task features relevant to adaptation, including feedback availability and session length, correlate with reduced illusion effects (Bruno and Franz, 2009; Schenk, Franz, and Bruno, 2011). However, direct evidence for or against adaptation effects is extremely limited, in part because so few studies have performed temporal analyses. Moreover, the small set of studies that *have* analyzed the time course of illusion effects on grasping contains conflicting findings: Franz, Fahle, Bülthoff, and Gegenfurtner (2001) reported a consistent Ebbinghaus illusion effect over time, whereas Whitwell, Buckingham, Enns, Chouinard, and Goodale (2016) reported a clear decrement in the Ponzo illusion effect. Although previous grasping research has confirmed that adaptation does occur, a more detailed theoretical account is needed to explain conflicting results like these.

In the present work, we developed a model of the trial-by-trial dynamics of grasp planning and adaptation, which can be used to obtain adaptation rate estimates across different task conditions. In addition, the model incorporates a mechanism that can explain why illusion effect decrements occur in some studies (*e.g.* Whitwell et al., 2016) but not others (*e.g.*, Franz et al., 2001). Specifically, we noticed that Whitwell et al. (2016) systematically presented the size-increasing and size-decreasing contexts of the Ponzo illusion at two different target locations while Franz et al. (2001) presented the two contexts of the Ebbinghaus illusion at a single target location. Another recent study also failed to find a decrement in the Müller-Lyer illusion effect on grasping when both contexts were presented in a single location, despite finding a decrement when sessions involved only one illusion context (Kopiske, Cesanek, Campagnoli, and Domini, 2017). These results suggest that the visuomotor mapping for grasp planning can be differentially adapted at separate spatial locations to compensate for the opposing visual distortions. In contrast, when opposing error signals are experienced at the same location, they will destructively interfere with one another. A similar capacity has been demonstrated for reach adaptation (Pine, Krakauer, Gordon, and Ghez, 1996; Ghahramani et al., 1996), but for grasping the proper adjustment is more complicated due to the presence of *two* perturbed contact points at each target location.

These considerations led us to develop a model that could account for trial-by-trial changes and would allow concurrent maintenance of multiple visuomotor mappings with varying degrees of inter-dependence. The model contains three components that are activated in sequence during a grasping movement. First, the *grasp planning* component determines the intended grasp trajectory based on two key variables: the visually perceived object size and a modifiable internal state linked to the active visuomotor mapping. Next, in the *error detection* component, an error signal is registered by comparing sensory feedback from the movement to the planned grasp trajectory. At the onset of a visual perturbation, the actual movement trajectory will necessarily deviate from the planned trajectory. Finally, the detected error automatically causes a proportional change in the internal state(s) through the *state update* component, altering subsequent grasp planning. In sum, our model combines a classic model of grasp planning that maps size information onto desired grip apertures (Jeannerod, 1984) with a dynamical system model of visuomotor adaptation known as a linear state-space model (Thoroughman and Shadmehr, 2000; Cheng and Sabes, 2006); see Methods for details. State-space models have been influential in research on reach adaptation, neatly accounting for various adaptation phenomena including error correction rates, forgetting, and interference between different visuomotor mappings (Smith, Ghazizadeh, and Shadmehr, 2006; but *cf.* Zarahn, Weston, Liang, Mazzoni, and Krakauer, 2008)

### 1.3. Overview of experimental design

In Experiment 1, we aimed to replicate previous findings of grasp adaptation and to test the capacity of the proposed model to capture trial-by-trial error corrections. We analyzed the adaptive response to positive and negative size perturbations using traditional aftereffects as well as model-estimated error correction rates. The size perturbations were 5-mm vertical expansions or contractions of each object in the visual scene, including the visual feedback of the fingertips (*i.e.*, index finger and thumb were drawn 2.5 mm above and below their respective physical locations for a positive perturbation, and vice versa for a negative perturbation).

In Experiment 2, we tested whether the visuomotor mapping for grasping can simultaneously adapt to positive and negative size perturbations when they are experienced in separate regions of space, which could explain some instances of illusion-resistant grasping. The ability to adapt to spatially separate opposing perturbations is a direct consequence of the spatial tuning of the visuomotor mapping, a feature that is easily quantified by our model. We compared model parameters and traditional aftereffects when the perturbation locations were separated by 80 mm ($\approx$ 11 degrees of reach angle) and when they were separated by 135 mm ($\approx$ 22 degrees of reach angle). We expected the 135-mm separation to be sufficient for adaptation to opposing perturbations based on the reach adaptation results of Ghahramani et al. (1996). By comparing a large-separation condition with a small-separation condition, instead of with a no-separation (*i.e.*, single-location) condition, we ensured that measured differences would be due to the separation distance and not the presence versus absence of two distinct locations "on top" and "on bottom". According to our spatial-separation hypothesis, we predicted greater aftereffects and reduced error-generalization parameters in the 135-mm condition compared to the 80-mm condition.

Our analysis focused exclusively on the maximum grip aperture (MGA), a kinematic landmark that occurs at the transition between grip opening and grip closure (Jeannerod, 1984; Smeets and Brenner, 1999). Some have criticized the assumption that the MGA reflects the size estimate used for grasp planning, contending that planning is actually based on estimates of the egocentric positions of the finger and thumb contact points (Smeets and Brenner, 1999, 2006). However, since we aimed to measure changes in the state of the visuomotor mapping, not the underlying visual estimates, the MGA is a reasonable choice of dependent variable, and it is compact and uncomplicated to analyze, unlike continuous grip aperture trajectories.

## 2. Materials and methods

### 2.1. Participants

One hundred thirty-seven participants were recruited from Brown University; see Table 1 for their distribution across the four experiments. We were unable to perform a reliable power analysis due to a lack of prior information about effect sizes, so we aimed to recruit