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Target modality affects visually guided online control of reaching

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ABSTRACT

The integration of vision and proprioception for estimating the hand's starting location prior to a reach has been shown to depend on the modality of the target towards which the reach is planned. Here we investigated whether the processing of online feedback is also influenced by target modality. Participants made reaching movements to a target that was defined by vision, proprioception, or both, and visual feedback about the unfolding movement was either present or absent. To measure online control we used the variability across trials; we examined the course of this variability for the different target modalities and effector conditions. Our results showed that the rate of decrease in variability in the later part of the movements (an indicator of online control) was minimally influenced by effector vision when participants reached towards a proprioceptive target, whereas the rate of decrease was clearly influenced by effector vision when participants reached towards a visual target. In other words, when participants reached towards a proprioceptively defined target they relied less on visual information about the moving hand than when they reached towards a visually defined target. These results suggest that target modality influences visual processing for online control.

1. Introduction

Much of what we know about the online control of reaching is based on the analysis of reaches to visually defined targets. We know considerably less about how online control operates for movements to targets that are defined proprioceptively, even though many of our daily movements involve proprioceptive location coding (i.e., any time we touch a part of our body). Such coding may even contribute to the localization of external visual objects that we have recently touched (Smeets et al., 2006). In the present study we took a closer look at the online characteristics of reaches to visual vs. proprioceptive targets. Our goal was to see whether target modality influences how visual information about the effector is used online.

1.1. Target modality influences reach planning

The modality of a reach target influences how people use multisensory information about their effector for planning movements: proprioceptive information about the effector's starting location is less important than visual information when people reach to a visual target, but more important when they reach to a proprioceptive target (Sarlegna & Sainburg, 2006; Sober & Sabes, 2005). For instance, when Sarlegna and Sainburg (2006) provided participants with shifted visual feedback about their reaching hand's starting location, the visual shift had a large effect on the subsequent reach if participants were reaching to a visual target. When they reached to a proprioceptive target (i.e., the other hand), however, the shifted visual feedback had a relatively small effect on the reach. Sober and Sabes (2005) have argued that a change in sensory weighting as a function of target modality is caused by the sensorimotor system's desire to avoid the noise created when sensory input is transformed from one coordinate frame to another. If the system can calculate the reach plan between the effector and the target by relying predominantly on the comparison of visual-to-visual or proprioceptive-to-proprioceptive coordinates, it will do so.

In light of the evidence that multisensory contributions to hand position estimation during reach planning depend on target modality, it is plausible that target modality would also influence hand position estimation as the reach unfolds. For such a modality-dependent re-weighting to occur, however, proprioception and vision would have to be potential sources of reliable information when the hand is in flight; we next briefly review evidence that that is the case.

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1.2. Proprioception and online control

Several studies have provided indirect evidence that proprioception plays an important role in the online correction of reaching movements. Movement corrections to perturbed targets have been shown to occur when participants have no vision of their hand and no awareness that the target was perturbed (Goodale, Pelisson, & Prablanc, 1986; Prablanc & Martin, 1992; Prablanc, Pelisson, & Goodale, 1986), suggesting that real-time proprioceptive information might be used for calculating online error between the hand and target. However, it is theoretically possible that such corrections are mediated entirely by efference copy-based mechanisms, wherein the sensorimotor system predicts the current location of the hand based on the prior motor command, and then makes online corrections using that prediction-based estimate. There is some empirical evidence that online corrections can be made in the absence of both vision and proprioception (Bard et al., 1999), suggesting that position estimation based on efference copy does play a role in online control; however, there are large differences in trajectory correction efficiency between control participants and a patient without proprioception (Sarlegna et al., 2006). This suggests that proprioception normally contributes to online estimates of the reaching hand. Indeed, it is plausible that proprioception, vision, and efference copy are integrated to maximize precision of the online estimate (Desmurget & Grafton, 2000; Wolpert, Ghahramani, & Jordan, 1995).

Recent work (Gosselin-Kessiby, Kalaska, & Messier, 2009; Gosselin-Kessiby, Messier, & Kalaska, 2008) has provided further support for the importance of proprioception to online control. In these studies participants completed a task analogous to inserting a letter into a postbox with changing slot orientations. One of the key findings was that participants re-oriented the angle of the 'letter' online to match the angle of the slot, even when they were instructed to maintain the orientation that the letter had at the start of the reach. This automatic online correction occurred even when participants had only proprioceptive information about both the angle of the slot and the angle of the letter. In fact, these studies are so far the only ones (to our knowledge) that have directly examined the online control of reaches to a proprioception-based target, and they suggest that online corrections of hand orientation can occur when proprioception is the only sense available.

1.3. Visual feedback and online control

The importance of vision to the online control of reaching has been easier than proprioception for researchers to investigate because of the experimental ease of removing or manipulating visual feedback about the effector. Experiments that have manipulated the availability of hand vision during reaching have shown that vision improves movement accuracy and precision (e.g., Keele & Posner, 1968; Prablanc et al., 1979; Woodworth, 1899; and see Elliott, Helsen, & Chua, 2001 for a review). Perturbation studies have shown that when visual information about the effector is unpredictably perturbed during the reach, people are able to rapidly compensate for the perturbations, even when these are not consciously detected (Brière & Proteau, 2010; Sarlegna et al., 2004; Saunders & Knill, 2003, 2005). In other words, vision is clearly useful for the online control of reaches to visual targets; however, its usefulness for reaches to proprioceptive targets is not fully understood.

1.4. Does target modality influence online visual processing?

To test whether target modality influences real-time visual processing of the effector we manipulated three factors: proprioceptive target, effector vision, and vision of the target during the reach. We were interested in the potential interaction between target modality and effector vision, and we hypothesized that effector vision would be used less for online control when the target was proprioceptively defined compared to when the target was visually defined. We were specifically interested in the pattern of movement variability over time. If a proprioceptive target reduces online visual processing of the effector, we should see less of an influence of effector vision on late movement variability when the target is proprioceptively defined. This reasoning is described in more detail in the next section.

1.5. Disentangling online and offline effects of vision: a note on analysis

When participants receive visual feedback about their unfolding movement, they can use that information in two ways: (1) to correct the ongoing movement if time permits, and (2) to improve performance on the subsequent trial. Disentangling these contributions to performance can be achieved by analyzing the position variability across trials at different kinematic markers and comparing the variability profiles in vision and no-vision conditions (Khan et al., 2003, 2006). A greater decrease in variability towards the end of the movement when visual feedback is available has been used to infer online use of vision; an overall difference in variability, without a difference in profile shape, has been used to infer offline use of vision. For instance, overall variability may be lower for fast visual closed-loop movements than for fast visual open-loop movements due to refinement of motor programming based on visual feedback obtained on the previous trial (Khan et al., 2003, 2006). Accordingly, if the ratio between variabilities in vision and no-vision conditions is relatively constant from the start to the end of the movement, one can infer primarily offline visual processing. If the ratio declines as the movement progresses (i.e. faster rate of variability decrease in vision trials than no-vision trials), one can infer that visual information was used online. This analysis assumes that increasing variability reflects feedforward processing (motor noise), while subsequent decreasing variability reflects feedback processing.

We have taken the time to explain the variability analysis because it is important for understanding the online and offline effects of real-time hand vision in our study. We did not perturb visual feedback, and so we required an analysis technique that was sensitive to subtle differences in performance across conditions. If there is reduced online visual control when the target is proprioceptively defined, this analysis should reveal a flatter vision-to-no-vision variability ratio when there is a proprioceptive target.

2. Methods

2.1. Participants

Eight participants from the University of Barcelona (3 female, ages 24–35), including the first author, took part in the study. Two participants were self-described left-handed, and for these participants the stimulus display was reversed, such that movements could be executed with the dominant hand. The study was approved by the local ethics committee, and participants provided informed consent.

2.2. Apparatus

The experiment was conducted in a dark room. Movements were executed with a stylus on a digitizing tablet (Calcomp DrawingTablet III 24240), which sampled the position of the stylus at a