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KEEP YOUR HEAD ON STRAIGHT: FACILITATING SENSORI-MOTOR TRANSFORMATIONS FOR EYE–HAND COORDINATION

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Abstract—In many day-to-day situations humans manifest a marked tendency to hold the head vertical while performing sensori-motor actions. For instance, when performing coordinated whole-body motor tasks, such as skiing, gymnastics or simply walking, and even when driving a car, human subjects will strive to keep the head aligned with the gravito-inertial vector. Until now, this phenomenon has been thought of as a means to limit variations of sensory signals emanating from the eyes and inner ears. Recent theories suggest that for the task of aligning the hand to a target, the CNS compares target and hand concurrently in both visual and kinesthetic domains, rather than combining sensory data into a single, multimodal reference frame. This implies that when sensory information is lacking in one modality, it must be 'reconstructed' based on information from the other. Here we asked subjects to reach to a visual target with the unseen hand. In this situation, the CNS might reconstruct the orientation of the target in kinesthetic space or reconstruct the orientation of the hand in visual space, or both. By having subjects tilt the head during target acquisition or during movement execution, we show a greater propensity to perform the sensory reconstruction that can be achieved when the head is held upright. These results suggest that the reason humans tend to keep their head upright may also have to do with how the brain manipulates and stores spatial information between reference frames and between sensory modalities, rather than only being tied to the specific problem of stabilizing visual and vestibular inputs.

Key words: human motor control, optimal sensori-motor integration, multimodal perception, head posture, virtual reality.

INTRODUCTION

When performing goal-directed hand movements the CNS combines sensory information about target and limb to maximize movement precision (van Beers et al., 1996, 1999; Ernst and Banks, 2002; Sober and Sabes, 2005; Smeets et al., 2006). More recently it has been proposed that when both target and hand can be sensed via multiple sensory modalities (e.g. visual and kinesthetic) the CNS achieves this integration of sensory information by carrying out comparisons of target and hand within each sensory modality and then combines the individual differences according to principles of maximum likelihood estimation to drive the hand to the target (Fig. 1a; c.f. McGuire and Sabes, 2009; Sabes, 2011). When target and hand are not perceived by the same sensory modality (e.g. when reaching with the unseen hand toward a visual target, see Fig. 1b), this formulation for eye–hand coordination implies that the CNS 'reconstructs' sensory information across sensory modalities (Andersen et al., 1993; Pouget et al., 2002; Tagliabue and McIntyre, 2008, 2011; McGuire and Sabes, 2009). Thus, in the example given in Fig. 1b, the CNS would reconstruct a kinesthetic representation of the visual target to be compared with kinesthetic information from the hand, and the CNS reconstructs a visual representation of the hand to be compared with the visually acquired target. The CNS could perform either or both of these reconstructions.

In our recent study (Tagliabue and McIntyre, 2011) we had subjects perform a task of orienting the unseen hand to align it with a visual target presented at a given orientation in the fronto-parallel plane. We compared this to the case where they aligned a visual stimulus to the pronation–supination orientation of the unseen, outstretched hand (i.e. the kinesthetic target). We refer to these two conditions as V–K (visual target, kinesthetically guided response) and K–V (kinesthetic target, visually guided response) respectively. In both cases, we imposed a memory delay between the disappearance of the target and the initiation of the response, such that subjects had to align the response to a target orientation that was stored in memory. In order to test what combination of sensory information (visual or kinesthetic) was used to perform the task, we had subjects tilt the head during the memory delay period and on half the trials we used virtual reality to create a slight conflict between the rotation of the head and the rotation of the visual field. If subjects used primarily visual information to perform the task, they should have reproduced, on average, the remembered target angle *with respect to the visual surround* (i.e. slightly tilted from the target's orientation measured with

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Abbreviations: ANOVA, analysis of variance; K, kinesthetic; T, head tilted; U, head upright; V, visual.

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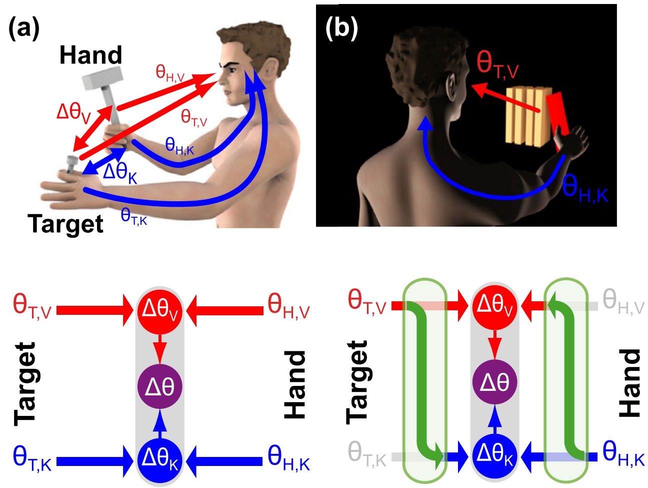

Fig. 1. (a) Concurrent comparison of target and hand in visual and kinesthetic space, when both target and hand can be seen and felt (e.g. using one hand to hammer a nail held with the other). Both uni-modal comparisons, $\Delta\theta_V$ and $\Delta\theta_K$, contribute to the final response $\Delta\theta$, weighted according to the relative variability of each. (b) Cross-modal transformations in a task of aligning the hand to a visual target, when kinesthetic feedback, but not visual feedback, is available about the hand's orientation (e.g. reaching for a visible object in an otherwise darkened room). Recurrent neural networks (Pouget et al., 2002) reconstruct kinesthetic information about the target $\theta_{T,K}$ from visual information about the target $\theta_{T,V}$ and a visual representation of the hand $\theta_{H,V}$ from kinesthetic signals about the hand $\theta_{H,K}$.

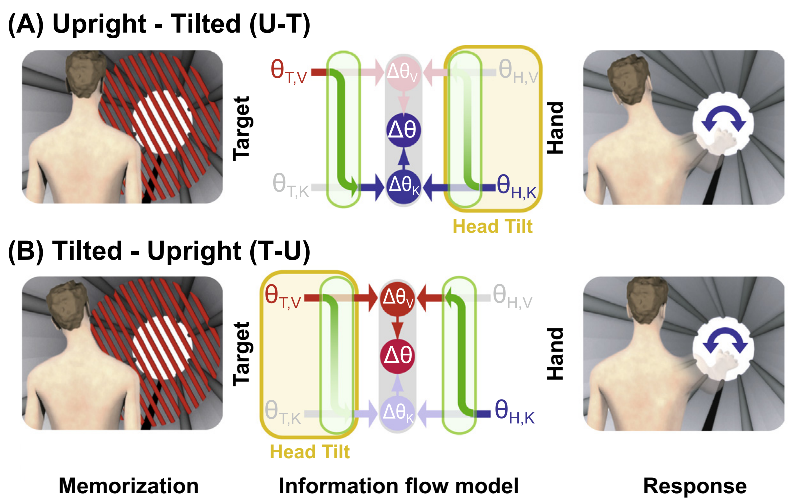

Fig. 2. Experimental conditions and predictions for our second hypothesis. (A) The target (red beams) is memorized with the head upright and the hand moves (prono-supinates) with the head tilted. (B) The target is memorized with the head tilted and the hand moves with the head upright. According to our second hypothesis, when the head is tilted (yellow areas in the model representations) the efficacy in reconstructing missing information is reduced, causing the brain to avoid these transformations. If the CNS simply gives greater emphasis to the sensory modality of the hand feedback, transformations will be conducted as in A, regardless of the head tilt conditions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

respect to gravity). On the other hand, if they used primarily kinesthetic information, they should have reproduced the remembered target angle *with respect to gravity and the body axis* (i.e. at a slight tilt from the target's orientation within the visual frame). We found that significant weight was given to visual information when the response was driven by visual feedback (K–V), while virtually no weight was given to a visual representation of the task when the manual response to a visual target was driven by kinesthetic feedback alone (V–K).

We can propose two hypotheses to explain this change in the weight given to visual representations between the V–K and K–V conditions. The first is that the CNS would give the greatest weight to sensory information that is directly available about the motor response. Thus, it would transform the visual target into kinesthetic space when responding with the unseen hand in V–K and it would transform the kinesthetic target (remembered hand posture) into visual space when the response involved the rotation of a visual line in K–V. The preference for transforming the target into the space of the response could arise from the temporal characteristics of the task: since the target disappeared before movement onset, its orientation could be transformed into hand space only once, at target