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Keep your head on straight: facilitating sensori-motor transformations for eye-hand coordination.

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Abstract

1
2 In many day-to-day situations humans manifest a marked tendency to hold the head
3 vertical while performing sensori-motor actions. For instance, when performing
4 coordinated whole-body motor tasks, such as skiing, gymnastics or simply walking, and
5 even when driving a car, human subjects will strive to keep the head aligned with the
6 gravito-inertial vector. Until now, this phenomenon has been thought of as a means to
7 limit variations of sensory signals emanating from the eyes and inner ears.
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12 Recent theories suggest that for the task of aligning the hand to a target, the CNS
13 compares target and hand concurrently in both visual and kinesthetic domains, rather
14 than combining sensory data into a single, multimodal reference frame. This implies that
15 when sensory information is lacking in one modality, it must be 'reconstructed' based on
16 information from the other. Here we asked subject to reach to a visual target with the
17 unseen hand. In this situation, the CNS might reconstruct the orientation of the target in
18 kinesthetic space or reconstruct the orientation of the hand in visual space, or both. By
19 having subjects tilt the head during target acquisition or during movement execution,
20 we show a greater propensity to perform the sensory reconstruction that can be
21 achieved when the head is held upright.
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31 These results suggest that the reason humans tend to keep their head upright may also
32 have to do with how the brain manipulates and stores spatial information between
33 reference frames and between sensory modalities, rather than only being tied to the
34 specific problem of stabilizing visual and vestibular inputs.
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1 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; 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 (Figure 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 Figure 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.

[Figure 1 about here]

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) were 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 reproduce, on average, the remembered target angle *with respect to the visual*

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surround (i.e. slightly tilted from the target's orientation measured with respect to gravity). On the other hand, if they used primarily kinesthetic information, they should reproduce 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 acquisition. Evaluating the motor error throughout the movement in the modality of the target would, however, require re-computing the transformation of the current hand position at each point in time.

The alternative hypothesis is that the CNS will select the sensory modality presenting the least variability, including any variability added by reconstructions necessary to operate in that modality (Tagliabue and McIntyre, 2008; McGuire and Sabes, 2009; Sabes, 2011; Tagliabue and McIntyre, 2011; Burns and Blohm al. 2010; for an interesting commentary, see Sober and Kording, 2012). As part of our previous protocol, the target was always acquired with the head upright and the response was always performed with the head tilted. Since tilting the head appears to increase the noise in sensorimotor transformations (McIntyre and Lipshits, 2008; Burns and Blohm al. 2010, Tagliabue and McIntyre, 2011) the CNS might therefore prefer to transform the target information into the sensory modality of the hand so as to perform the transformation while the head was still upright.

Both of the above hypotheses would predict that the target would be transformed into the modality of the hand feedback in our previous experiment, because the response

1 was always performed with the head tilted in those experiments. To differentiate
2 between them, here we had subjects align the unseen hand to visual targets (V-K) in two
3 different situations. In the U-T condition, subjects acquired the target with the head
4 upright (U) and then aligned the hand to the remembered target with the head tilted (T).
5 In T-U, subjects acquired the target with the head tilted, and oriented the hand while the
6 head was in an upright posture. If the CNS always works in the sensory modality of the
7 hand, we should observe no differences between U-T and T-U, because in both
8 conditions the only feedback about the hand orientation was kinesthetic. Conversely, if
9 the fact that head tilt degrades cross-modal transformations causes the CNS to prefer
10 reconstructions performed with the head upright, responses in the U-T condition should
11 be mainly driven by kinesthetic information, whilst in the T-U condition visual
12 information should be given more weight, as illustrated in Figure 2.
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22 [Figure 2 about here]
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25 **2 Experimental Procedures**

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27 The experimental setup was the same as in our previous studies (Tagliabue and
28 McIntyre 2011-12). The position and orientation of the subject's head was acquired by a
29 motion capture system (Charnwood Dynamics Ltd.) and used in real time to update the
30 visual scene viewed by the subject in virtual-reality goggles (nVisor sx60, Nvis). The
31 measured position and orientation of the hand were also used when necessary to depict
32 it in the scene. The virtual environment consisted of a cylindrical horizontal tunnel
33 whose walls were marked by longitudinal stripes parallel to the tunnel axis. These
34 stripes helped the subjects to perceive their own spatial orientation in the virtual world.
35 Identifying the visual vertical was facilitated by the fact that the stripes went from white
36 on the ceiling to black on the floor.
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47 **2.1 Experimental conditions**

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49 In both experimental conditions subjects had to reproduce the orientation of a
50 remembered visual target (red parallel beams in left part of Figure 2) by adjusting the
51 pronation-supination of their unseen hand (represented as transparent in the right part of
52 Figure 2), as in the V-K condition of our previous study (Tagliabue and McIntyre 2011).
53 The U-T condition was a replica of our previous V-K condition: subjects memorized the
54 targets with the head upright and oriented the hand with the head tilted. On the other
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1 hand, in the T-U condition subjects memorized the visual target with the head tilted and
2 responded with the head upright.

3 *U-T:* Subjects started a trial with the head upright. They observed parallel beams
4 projected in the fronto-parallel plane in different orientations with respect to the
5 vertical (the beams are represented in red in the left part of Figure 2). Subjects had 2.5
6 sec to memorize the orientation of the beams before they disappeared. Subjects then
7 had 5 sec to tilt their head by 15° to the right or to the left, depending on the trial. To
8 guide subjects to the desired inclination of the head, the color of the tunnel turned from
9 red to green as the head approached the desired inclination. They also heard a sound
10 with a left-right balance corresponding to the direction of the desired head inclination,
11 which decreased in volume as the head approached 15°. If the subject was unable to
12 extinguish the sound and make the tunnel turn green within 5 sec, the trial was
13 interrupted and was repeated later on. If the desired head inclination was attained, the
14 subject was prompted to align the unseen hand with the remembered target orientation
15 by changing its prono-supination angle, and to record the response by pressing a button
16 with the other hand.
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18 *T-U:* Subjects started the trial with the head upright, but the visual target did not appear
19 until they tilted the head by 15°. The subject was guided to the desired head angle by the
20 same color and sound cues described above. Once the subject reached the desired head
21 inclination, the beams were displayed for 2.5 sec, after which they disappeared and the
22 color and sound cues instructed the subject to return their head to the upright position.
23 If the subjects were able to do so in 5 sec, they were allowed to raise their arm to align
24 their unseen hand to the memorized target.
25

26 *Sensory Conflict:* To measure the weight given to visual versus kinesthetic information
27 when performing the response, we introduced a conflict between these two sensory
28 modalities during the memory delay. Tracking of the virtual-reality goggles was
29 normally used to hold the visual scene stable with respect to the real world during
30 movements of the head. But in half of the trials the amplitude of the angle between the
31 visual vertical and gravity varied imperceptibly during the actual head tilt,
32 proportionally by a factor of 0.6. Thus, when the head tilted 15°, the subject received
33 visual information corresponding to a rotation of 24°, resulting in a conflict of about 9°.
34 When the head was upright, there was no conflict. The values of 15° nominal head tilt
35 and a conflict factor of 0.6 were chosen based on pilot experiments which showed that
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this amount of conflict led to measurable deviations of the motor response, even though when asked after the experiment subjects did not report noticing the effects of the conflict. The ability to create this conflict without the subjects being consciously aware of it may be due to the fact that during active movement the semicircular canals and proprioceptive signals do not perfectly update spatial representations (Blouin et al 1998), even if that updating is significantly more effective when otolith cues can be used (Klier et al. 2005).

We then measured systematic deviations in responses when the conflict was present, compared to the non-conflict trials, as a means to measure of the weight given to the visual information. A deviation of 0% would mean that subjects ignored the deviation of the visual surround and produced a response in a kinesthetic (and gravitational) reference frame. A deviation of 100% would indicate that subjects responded with a hand orientation at the same angle with respect to the visual surround, which would indicate that the subjects relied completely on visual information, ignoring a representation of the target in a kinesthetic reference frame.

2.2 Participants

After giving written informed consent, 16 subjects (8 male and 8 female, average age 31 ± 10) participated to this study, which was reviewed and approved by the Paris Descartes University Institutional Review Board. All subjects performed both experimental procedures; half of them starting with U-T and the other half with T-U. For each of the two conditions subjects performed 56 trials: two for each combination of seven target orientations (-45° , -30° , -15° , 0° , $+15^\circ$, $+30^\circ$, $+45^\circ$), two head inclinations ($\pm 15^\circ$), and two levels of conflict (no and yes).

2.3 Data analysis

We analyzed the data in terms of alignment errors between hand and target at the moment of the response. To quantify the effect of the sensory conflict in each condition, we adapted the data analysis used in our previous study (Tagliabue and McIntyre, 2011), collapsing data across head tilt directions, target orientation and different level of conflict, as follows. First, to compensate for any global rotation of responses, due for example to possible Aubert or Muller effects (see Howard, 1982), we subtracted from all responses involving head tilt to the right with and without conflict the average of the responses to the 0° target in the trials without conflict and we did the same for left tilt,

1 on a subject-by-subject basis. Next, for each response with conflict we computed the
2 deviation from the mean of all responses without conflict and we expressed this
3 deviation as percentage of the expected deviation if only visual information was used (= $0.6 \times$
4 head angle), taking into account the amount of actual head tilt measured on each
5 trial. Finally, we computed the mean value of these percentage deviations, to
6 characterize the overall weight given to the visual information for each subject and for
7 each condition. We used ANOVA for repeated measures to test for differences in
8 response deviations (relative weighting) between U-T and T-U conditions. We used
9 Student's t-test to ascertain whether the response deviations induced by the conflict
10 were significantly different from the purely kinesthetic response (0%) or from the
11 purely visual response (100%).

12 The variability of the performance of each individual subject was also evaluated for the
13 trials without conflict. To robustly estimate each subject's variability, despite the fact
14 that only two responses could be used for each combination of target orientation and
15 head inclination, the following procedure was used. First, the responses with the head
16 tilted to the right and to the left were combined as reported above. Then, the variance,
17 σ^2_t , of the responses obtained for each of the 14 combinations of target orientation and
18 head orientations were combined to obtain a measure of response variability, taken as
19 the global standard deviation from multiple samples (McIntyre et al. 1997; Morrison
20 1990). The variability data, SD, were transformed by the function $\log(\text{SD}+1)$, before
21 performing the ANOVA (Luyat et al. 2005).

22 **3 Results**

23 The average responses to each target orientation are reported in Figure 3 for the U-T
24 and T-U condition separately. The similarity between the constant errors made by the
25 subjects in the U-T and T-U conditions for the trials without conflict (blue lines) suggests
26 that the participants were able to perform the task equally well in both conditions. This
27 observation is also supported by a similar variability of the response in the two
28 conditions (U-T: $7.61 \pm 1.3^\circ$; T-U: $6.97 \pm 1.2^\circ$; $F_{(1,15)}=0.004$, $p=0.95$).

29 On the other hand, responses in the trials with conflict (red lines in Figure 3) differ
30 markedly between the U-T and T-U conditions. The red arrows, representing the
31 deviations of responses due to the tilt of the visual scene, show that responses were
32 more deviated in the T-U than in the U-T condition.

[Figure 3 about here]

This is confirmed by Figure 4, which shows that in the U-T condition responses were not, on average, deviated by the sensory conflict (t-test with respect to 0%: $F=-0.75$, $p=0.46$), meaning that a kinesthetic representation of the task was used. On the other hand, in the T-U condition responses were significantly deviated by the conflict (t-test with respect to 0%: $F= 4.24$, $p= 0.0007$), although subjects' responses were not 100% captured by visual information (t-test with respect to 100%: $F= -3.73$, $p= 0.002$), they were not significantly different ($F= -1.89$, $p=0.08$) from the deviations of 77% that we observed, on average, in a purely visual task (V-V) in our previous study (Tagliabue and McIntyre 2011). ANOVA showed that the relative weight given to a visual representation significantly increased in T-U with respect to U-T condition ($F(1,15)=14.36$, $p=0.001$).

[Figure 4 about here]

4 Discussion

The main result is a striking difference in the effect of a sensory conflict on movements performed to align the unseen hand with a visual target, depending on whether the target orientation was memorized with the head upright and the hand moved with the head tilted to the side, or vice-versa. In the U-T condition, responses were not at all deviated by rotation of the visual scene, as we saw previously (V-K condition; see Tagliabue and McIntyre, 2011). In contrast, responses in the T-U condition relied more heavily on visual information, as indicated by the significant effect that rotations of the visual scene had on the responses. With respect to the computational model shown in Fig. 1, the difference between the U-T and T-U conditions rejects the idea that the brain simply prefers performing the target-hand comparison in the sensory modality of the hand feedback. Rather, one can more readily explain these data, within the context of this model, by a preference for transforming sensory information while the head is upright, i.e. transforming visual target information into kinesthetic space in U-T and kinesthetic hand information into visual space in T-U, as depicted in Fig. 2.

These results mirror a related study performed by Burns and Blohm (2010) where it was shown that when the head is tilted to the side, the CNS gives greater weight to visual versus proprioceptive information that was available about the hand during motor planning, compared to when the head was held upright. Conditions in our experiments differed somewhat from that study in that it was intrinsically cross modal. Subjects had

1 no visual information about the hand, yet they appeared to reconstruct one so as to
2 perform the task at least partly in visual space. They did so, however, only when the
3 head was held upright during movement execution (T-U). Tilting the head during
4 movement execution, but not target acquisition (U-T) had the opposite effect, privileging
5 the transformation of target information to allow a kinesthetic representation of the
6 task. Both the study reported here and that performed by Burns et Blohm (2010)
7 confirm the idea that tilting the head with respect to gravity disrupts sensorimotor
8 transformations, causing shifts in the weight given to visual or kinesthetic information
9 in sensorimotor tasks. We have interpreted our experimental data within the context of
10 two specific premises. The first is that the CNS performs parallel comparisons of target
11 and hand as shown in Fig. 1. While other hypotheses about the reference frames
12 employed by the CNS might explain the data presented here, the notion of multiple
13 internal reference frames tied to different sensory modalities has enjoyed considerable
14 support from recent experiments targeting this specific question (Droulez et al. 1993;
15 Pouget et al. 2002; Avillac et al. 2005; Smeets et al. 2006; Tagliabue and McIntyre 2008,
16 2011,2012; McGuire and Sabes 2009, Sabes 2011).

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29 The second is that sensory transformations are noisier when the head is tilted (McIntyre
30 and Lipshits 2008, Burns and Blohm al. 2010). Observations that drawing a shape
31 (Guerraz et al., 2003, 2011), pointing to visually memorized targets (Priour et al. 2006)
32 or aligning a visual stimulus to the direction of constrained movements of the hand
33 (McIntyre and Lipshits, 2008) were more variable when the head was tilted to the side,
34 provide support for this latter supposition. It is interesting to note, therefore, that
35 response variability in uni-modal kinesthetic (Luyat et al. 2001, McIntyre and Lipshits
36 2008) or visual (McIntyre et al. 2001, McIntyre and Lipshits 2008) tasks did not show
37 greater variability¹. This indicates that head tilt does not affect visual or haptic
38 perception *per se*. Rather, head tilt specifically affects cross-modal sensory
39 transformations.

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52 Reports of the perceived visual or haptic vertical were also more variable when the head
53 was tilted with respect to gravity (Schuler et al. 2010) and it has been shown that biases

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59 ¹ With the exception of the vertical and horizontal targets, which are affected by the so
60 called 'oblique effect'.
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in the perceived visual vertical could be predicted by a Bayesian model that supposes greater otolith variability for oblique head angles (De Vrijer et al., 2008; Tarnutzer et al., 2009). Noisy otoliths could therefore be the source of the increased variability in visuo-kinesthetic transformations that are performed when the head is tilted. But the aforementioned studies of human perception did not measure otolith outputs directly. Rather, they measured the subjects' reports of the perceived visual vertical. In as much as providing the response about the perceived vertical requires sensorimotor transformations, the increased noisiness with head tilt could be due to noisier graviceptor inputs or to an intrinsic property of the transformation itself. Furthermore, in our experiments vestibular inputs were confounded with proprioceptive information from the neck. To fully implicate the vestibular system as a source of the increased variability, one should perhaps perform these tests a) on human subjects suffering from vestibular deficits, b) in the weightless environment of space flight, or c) in animal models. But in any case, the supposition that head tilt leads to noisier transformations, plus the parallel model structure of Fig. 1, provides a coherent explanation as to why subjects performed the visuo-kinesthetic matching task in visual space for T-U and in kinesthetic space in U-T.

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Head tilt also appears to perturb ocular-motor responses to visual stimuli, which are more variable when the head is tilted (Gizzi et al. 1994) and similar effects of head tilt have been observed in more cognitive tasks, such as verbally describing the location of a visually memorized target (Prieur et al. 2006) or identifying ambiguous alphabetic characters (Dyde et al. 2006). These phenomena are likely to be related to the interactions between sensory signals generated by head tilt (Bremmer et al. 2002; Sclack et al. 2002; Indovina et al. 2005) and the neural networks that are thought to carry out transformations between visual and kinesthetic information in the parietal cortex (Pouget et al. 2002; Avillac et al. 2005). That sensory signals related to the amount of head tilt may be involved in sensori-motor transformations could explain why patients with vestibular deficits have difficulties integrating non-vestibular cues in tasks of spatial navigation (Borel et al., 2008).

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The negative impact of head-tilt on one's ability to perform sensory transformations provides new insight into the ontogenesis of head stabilization mechanisms in humans

1 (Pozzo et al. 1990, 1995; Assaiante and Amblard, 1993; Bril and Ledebt, 1998; Cromwell
2 et al. 2001). Improving the quality of sensorimotor transformations may in fact underlie
3 the tendency to flex the neck to compensate for body lateral tilt (Prieur et al. 2006), for
4 the tilt of the gravito-inertial force during off axis centrifugation (Prieur et al. 2005) or
5 when a steering car (Zikovitz and Harris, 1999). Indeed, this compensatory behavior has
6 been observed mainly when the subject is occupied in a sensory-motor task: i.e. the
7 driver, but not the passenger, tilts the head in the direction of steering (Zikovitz and
8 Harris, 1999). Moreover, if the passenger is instructed to actively tilt the head to
9 compensate for centrifugal forces, the severity of motion sickness decreases (Wada et al.
10 2012), suggesting an enhanced capacity to match visual and vestibular information
11 under these conditions.
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21 5 Conclusions

22 We have shown that when aligning the unseen hand to a visual target, the CNS does not
23 have an *a priori* preference for performing the task in kinesthetic space. The CNS instead
24 privileges the sensory modality and coordinate space that minimizes response
25 variability, according to the principles of maximum likelihood estimation. In doing so we
26 provide additional support for the idea that the CNS performs multiple, concurrent
27 comparisons of target and hand in both visual and kinesthetic space (Tagliabue and
28 McIntyre 2008, 2011; McGuire and Sabes 2009, Sabes 2011) and for the idea that head
29 tilt degrades, and thus de-emphasizes information that is transformed between sensory
30 modalities (Burns and Blohm 2010). Furthermore, we have discussed these results with
31 respect to a variety of previous studies in which a propensity to maintain the head
32 upright has been observed. Specifically, we contend that head stabilization may be
33 motivated as much by the improvements in sensori-motor transformations that occur
34 when the head is aligned with gravity as by a desire to minimize variations in vestibular
35 and visual inputs themselves. In this sense we have provided experimental confirmation
36 of Paillard's (1991) intuition that gravity serves as unifying and invariant reference
37 around which the other sensory modalities would be organized.
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Figure Legends

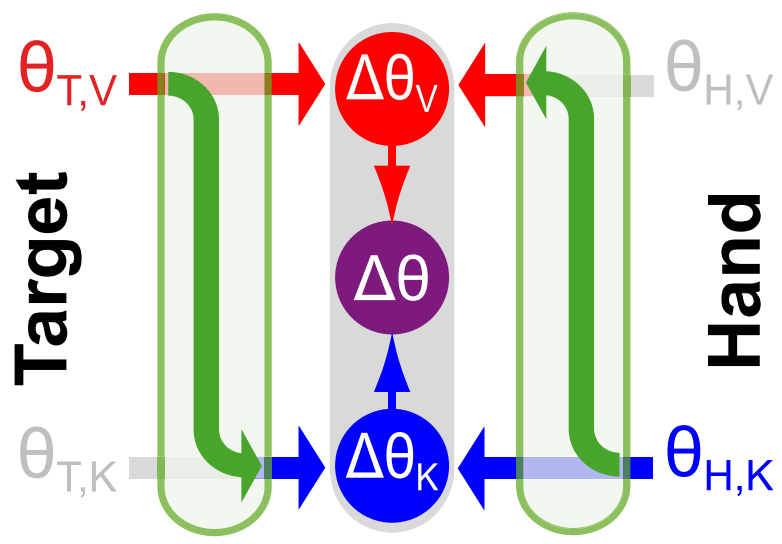
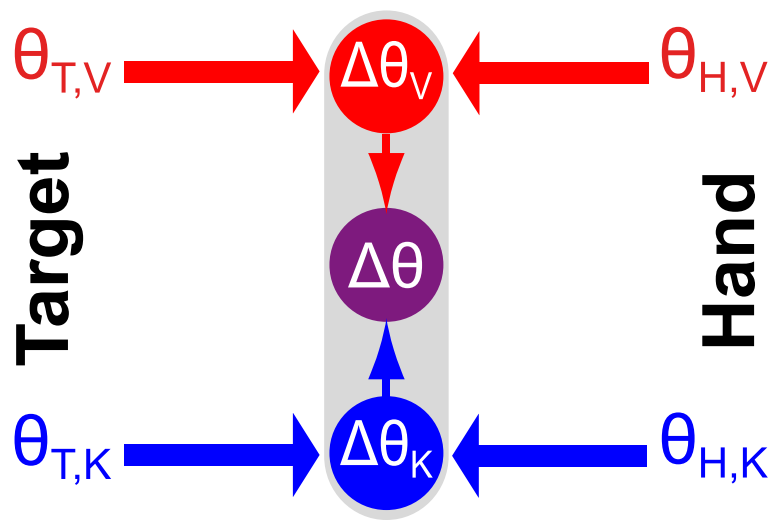
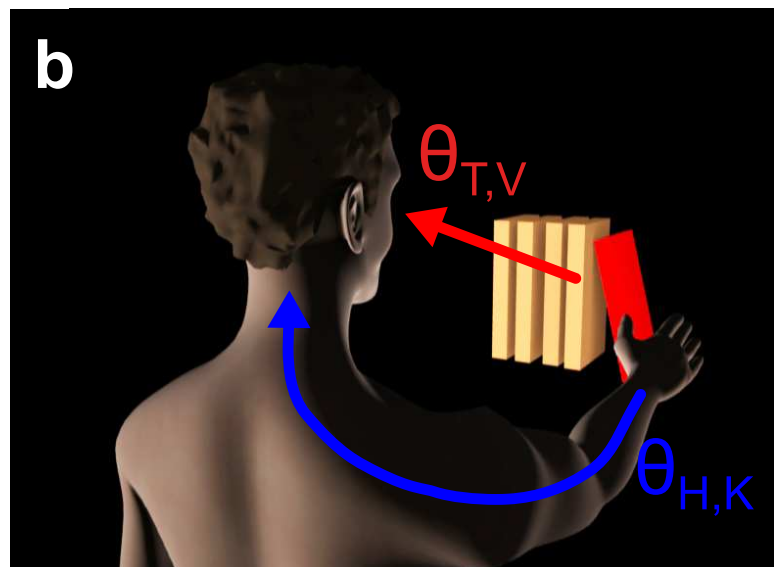
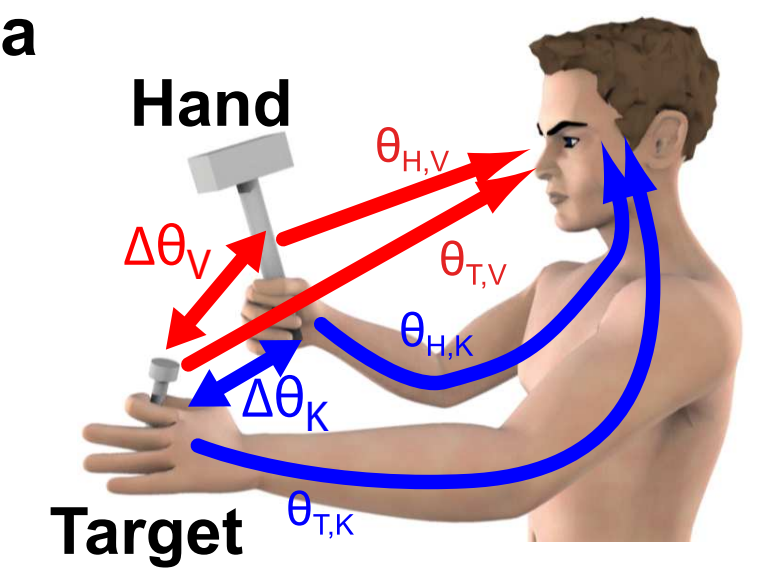
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3 *Figure 1: (a) Concurrent comparison of target and hand in visual and kinesthetic space, when both target*
4 *and hand can be seen and felt (e.g. using one hand to hammer a nail held with the other). Both uni-modal*
5 *comparisons, $\Delta\theta_V$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

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17 *Figure 2: Experimental conditions and predictions for our second hypothesis. A) The target (red beams) is*
18 *memorized with the head upright and the hand moves (prono-supinates) with the head tilted. B) The target*
19 *is memorized with the head tilted and the hand moves with the head upright. According to our second*
20 *hypothesis, when the head is tilted (yellow areas in the model representations) the efficacy in reconstructing*
21 *missing information is reduced, causing the brain to avoid these transformations. If the CNS simply gives*
22 *greater emphasis to the sensory modality of the hand feedback, transformations will be conducted as in A,*
23 *regardless of the head tilt conditions.*

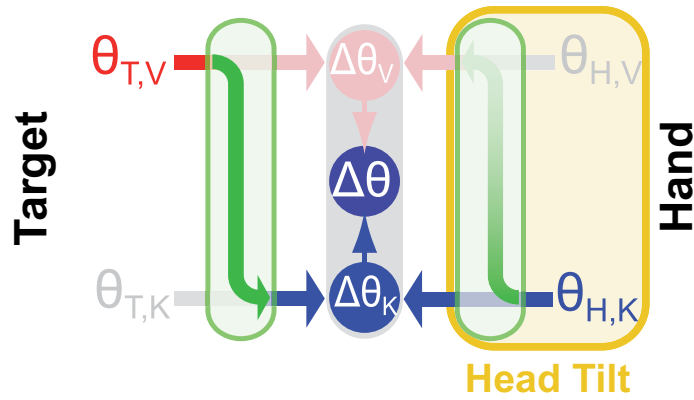
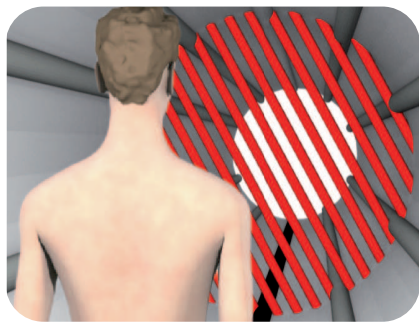
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29 *Figure 3: Subject response to each target orientation in the U-T and T-U conditions. The responses for the*
30 *trials with and without conflict are represented separately. Thick lines are the average responses*
31 *(transparent areas' width represent the standard error) of all subjects and combine trials with left and right*
32 *head tilt, as explained in the methods section. The thick arrows on the top of each panel represent the*
33 *measured deviations due to the tilt of the visual scene. Thin arrows represent what would be the expected*
34 *deviation if the movement encoding were purely visual.*

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39 *Figure 4: Deviations induced by sensory conflict when the target was memorized with the head upright and*
40 *the response produced with the head tilted (U-T) and vice-versa (T-U). Deviations of 0% are to be expected if*
41 *subjects use only kinesthetic or gravitational information to align the response to the remembered target*
42 *orientation. Deviations of 100% would be expected if subjects aligned the response to the remembered target*
43 *orientation with respect to the visual scene. A value 77% is the response deviation that we obtained on*
44 *average in the purely visual condition (V-V) in our previous study. Vertical whiskers represent the 0.95*
45 *confidence intervals. Stars represent the significance of the main effects in the ANOVA and the results of the t-*
46 *test comparison with the nominal 0% and 100% values. (***) $p \leq 0.001$.*

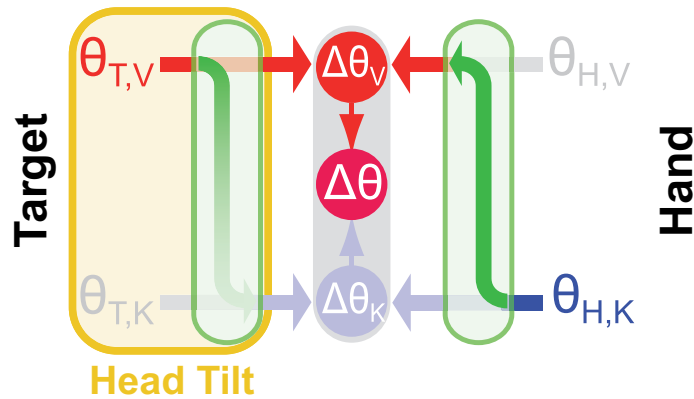
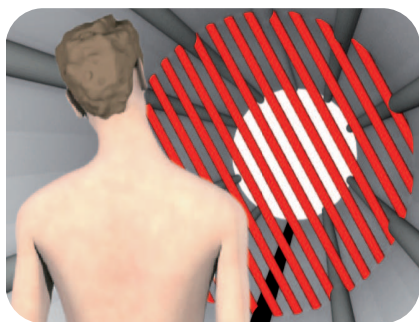
Figure 1
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A) Upright - Tilted (U-T)



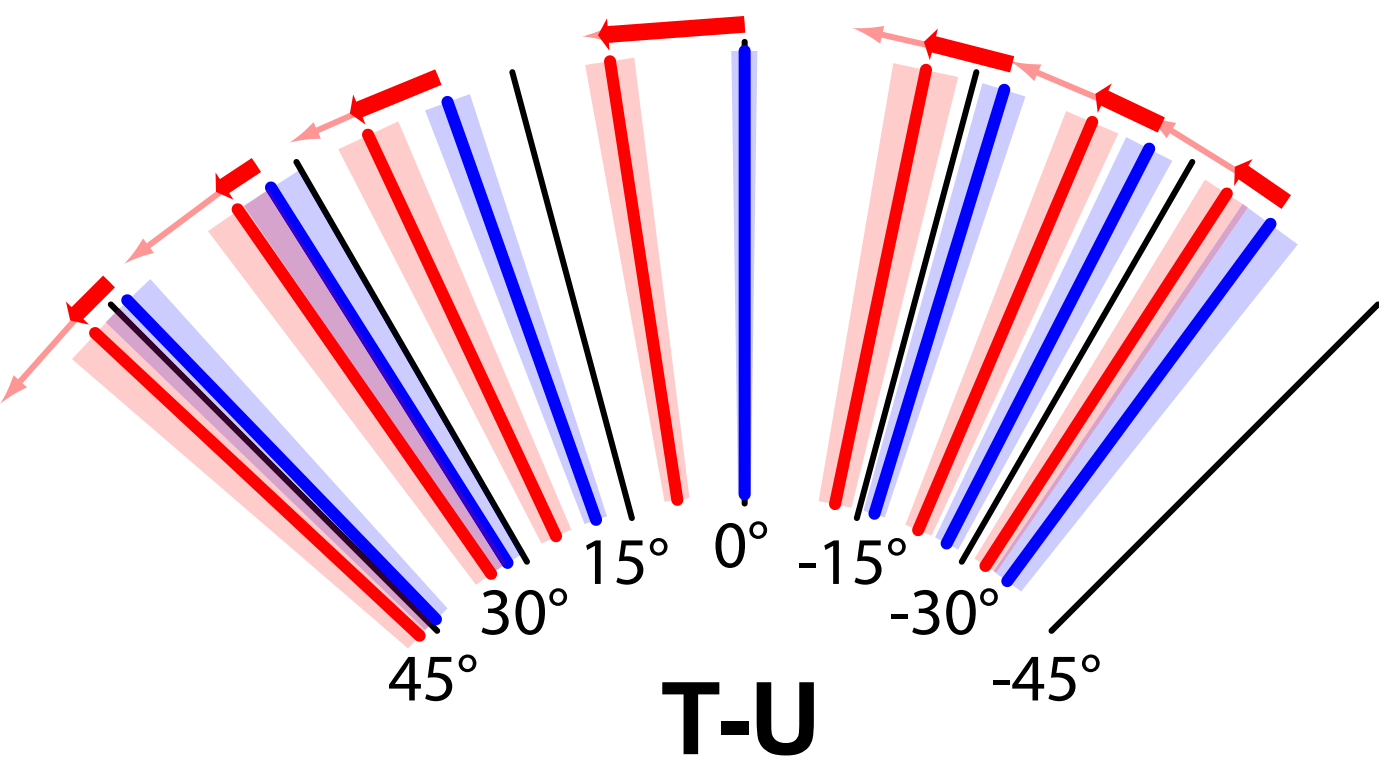
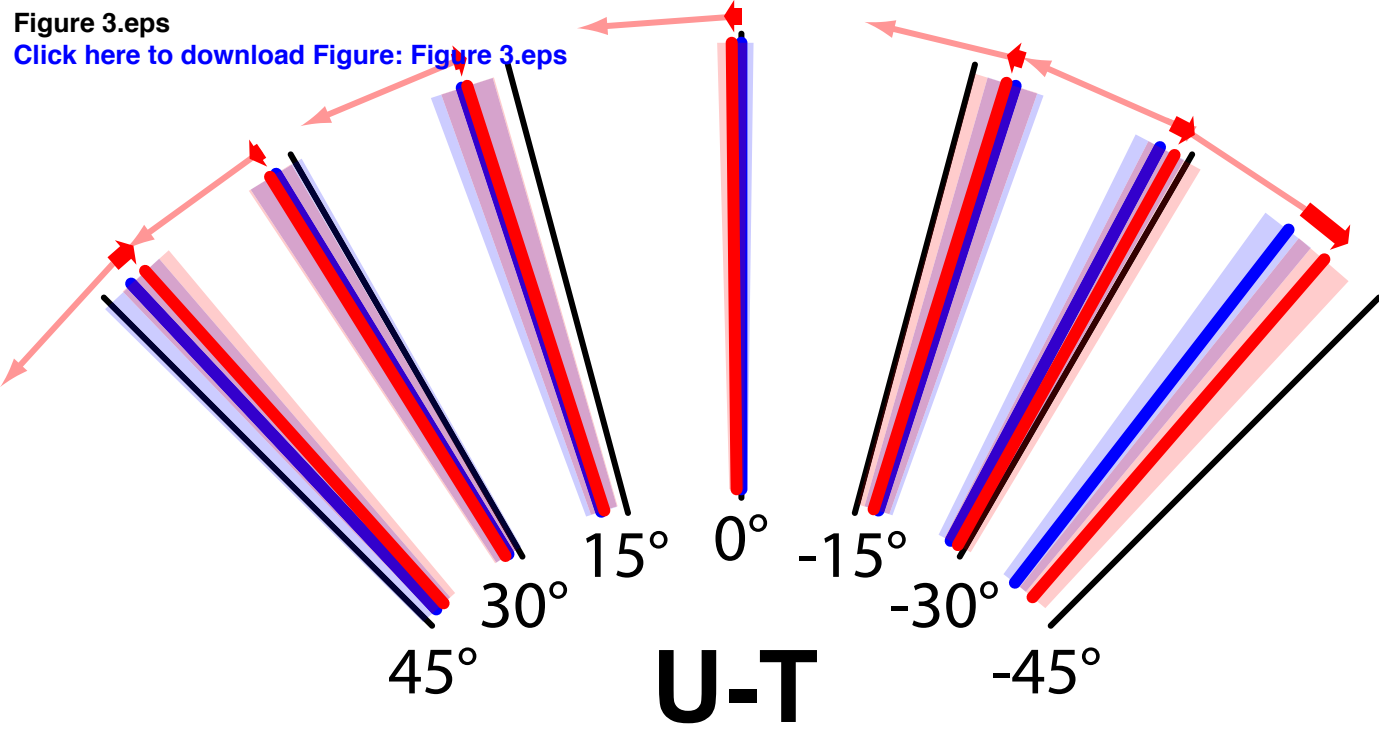
B) Tilted - Upright (T-U)



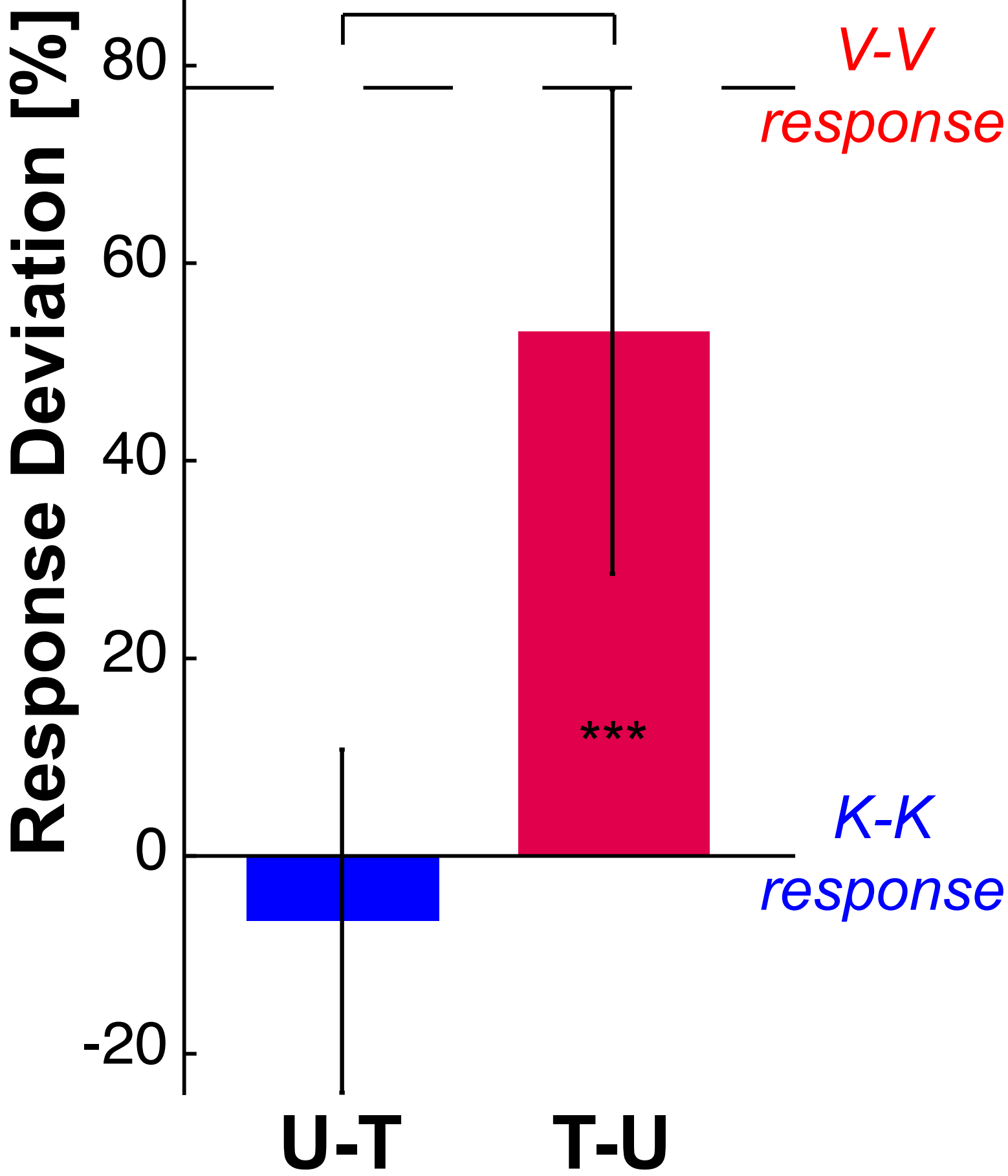
Memorization

Information flow model

Response



- Target
- No Conflict
- Conflict
- ← Theoretical Deviation
- ← Observed Deviation



Highlights

- Subjects aligned the hand to a visual target, i.e. an intrinsically cross-modal task.
- Subjects were asked to tilt the head in different phases of the task.
- Sensory conflict was used to identify sensory transformations that were performed.
- Subjects avoided performing visuo-kinesthetic transformations with the head tilted.
- Head stabilization might therefore serve to facilitate sensory transformations.