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Anticipatory Postural Adjustments associated to reaching movements are programmed according to the availability of visual information

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Abstract

During goal-directed arm movements, the eyes, head and arm are coordinated to look at and reach the target. We examined whether the expectancy of visual information about the target modifies Anticipatory Postural Adjustments (APAs).

Ten standing subjects had to i) move the eyes, head and arm so as to reach, with both gaze and index-finger, a target of known position placed outside their visual field (*Gaze-Reach*); ii) look at the target while reaching it (*Reach in Full Vision*); iii) keep the gaze away until having touched it (*Reach then Gaze*) and iv) just *Gaze without Reach* the target. We recorded eye, head, right arm and acromion kinematics, EMGs from upper- and lower-limb muscles and forces exerted on the ground. In *Gaze-Reach*, two coordination strategies were found: when gaze preceded arm muscle recruitment (*Gaze-first*) and when the opposite occurred (*Reach-first*). APAs in acromion kinematics, leg muscles and ground forces started significantly earlier in *Gaze-first* vs. *Reach-first* (mean time advance: 44.3 ± 8.9 ms), as it was in *Reach in Full Vision* vs. *Reach then Gaze* (39.5 ± 7.9 ms). The *Gaze-first* to *Reach-first* time-shift was similar to that between *Reach in Full Vision* and *Reach then Gaze* ($p=0.58$). Moreover, *Gaze without Reach* data witnessed that the head-induced postural actions did not affect the APA onset in *Gaze-first* and *Reach-first*.

In conclusion, in *Gaze-first* the central control of posture considers visual information while planning the movement, like in *Reach in Full Vision*; while *Reach-first* is more similar to *Reach then Gaze*, where vision is not required.

Keywords APAs, eye-hand coordination, motor control, posture, voluntary movement

Introduction

Anticipatory Postural Adjustments (APAs) are unconscious muscular activities, which have been originally considered as a way to counterbalance the expected perturbation induced by the primary movement (Massion 1992; Bouisset and Do 2008). However, in the last decade this view has been challenged, both experimentally and through simulations (Lee et al. 1990; Stapley et al. 1999; Commissaris et al. 2001; Pozzo et al. 2001; Leonard et al. 2009), leading to the idea that APAs actually contribute to the voluntary movement. For example, when pointing a target with the upper-limb, the recruitment of the arm prime mover is preceded by APAs, distributed to trunk and lower-limb muscles, which displace the Centre of Pressure (CoP) backwards, so as to drive the arm and the Centre of Mass (CoM) toward the target.

In agreement with this perspective, Caronni et al. (2013) suggested that APAs would not only guarantee the whole body equilibrium, but may also be important in refining the accuracy of pointing movements performed with the whole upper-limb. By using prismatic lenses, these authors induced a change in the subject's straight ahead, which was very effective in altering the motor program, so that the subject missed the target. In this experiment, it was observed that the pointing errors were associated to changes in the APAs only, without any significant change of the prime mover activity, i.e. of the voluntary command.

Data from Caronni et al. (2013) thus support the idea that APAs play an active role in determining the movement outcome, but also highlight a possible linkage between vision and APAs programming. The role of vision in the control of APAs was also proposed by Krishnan and Aruin (2011). In fact, when they exposed subjects to an external perturbation induced by a heavy pendulum, with or without holding onto a walker, they reported no significant differences in APAs when full vision was available. That result suggested that vision could overrule the proprioceptive information and/or the additional support in setting the anticipatory postural control to counteract the incoming external perturbation. In a similar experimental set-up, APAs were found to be greater when providing dynamic visual cues (high-frequencies strobe light) than static visual cues (low-frequency strobe light), supporting the importance of vision in the adaptation of APAs (Mohapatra and Aruin 2013). Finally, Mohapatra et al. (2012) illustrated the importance of visual acuity in a correct tailoring of APAs against an external perturbation. Indeed, the anticipatory postural control changed when asking subjects with normal vision to wear eye-glasses with negative or positive powered lenses.

However, on one hand the indirect suggestion that visual information affects APAs associated to voluntary movement (cfr. Caronni et al. 2013) was obtained under a highly unnatural vision condition; on the other, data from Aruin's group (Krishnan and Aruin 2011; Mohapatra et al. 2012; Mohapatra and Aruin 2013) dealt with APAs associated to external perturbation, not to voluntary movements. Therefore, we chose to analyze the relationship between vision and APAs in a more natural behaviour: a coordinated movement of eyes, head and upper-limb when reaching with the index-fingertip a target placed outside the visual field, i.e. a simultaneous gazing and arm reaching movement (*Gaze-Reach*). First of all, we asked subjects to familiarize with the fixed target, so as to memorize its position, because Frens and Erkelens (1991), as well as Carnahan and Marteniuk (1991), illustrated that the a-priori knowledge of target position can sometime anticipate the arm movement with respect to that of eyes and head. Therefore, we expected that also in our experiments two *Gaze-Reach* behaviours could be observed: one in which eyes and head started to move before the arm prime mover recruitment, i.e. *Gaze first*, and another in which the reaching activity started before the gaze, i.e. *Reach first*. In the first case, subjects would have already got the visual information about target position before starting the arm movement, while in the second case such information would have been postponed. Considering these two possibilities, it was also planned to perform two control conditions: i) keeping steadily the gaze on the target while reaching (*Reach in Full Vision*) and ii) keeping the gaze away from the target till having reached it with the index-finger, then freely look at it (*Reach then Gaze*). Note that in the first case there was full availability of visual information well prior to the arm movement (i.e. the extreme case of *Gaze first*) while in the second case the opposite occurred (i.e. the extreme case of *Reach first*). Moreover, in both control conditions the eyes and head were still throughout the arm movement. Altogether, this experimental paradigm allowed to separately evaluate the effect of vision availability on APAs, possibly ruling out the confounding factor of the postural perturbations linked to the head movements.

Taking into account that APAs and prime mover recruitment are controlled by a *shared* motor command (Stapley et al. 1999; Bruttini et al. 2014) and the proposal that eye and hand movements toward a target during simple pointing tasks are also driven by a common command (Gopal and Murthy 2015), our working hypothesis was that the temporal organization of APAs would have been subordinated to the control of eye movements.

Methods

Participants

Ten right-handed volunteers participated in this study (mean age \pm SD: 25.4 \pm 2.0 years). No subject had any history of orthopaedic or neurological disease and all of them gave their informed consent prior to their inclusion in the study. The procedure was carried out in accordance with the standards of the Declaration of Helsinki and approved by the local Ethical Committee.

Motor task

Subjects stood on a force platform according to their spontaneous upright stance, while keeping both upper-limbs along the body. After an acoustic go signal, delivered every 7 s, subjects were required to perform a ballistic reaching movement, i.e. a movement performed at will, but so quickly that once initiated it cannot be voluntarily changed. The instruction was to freely decide when starting the movement but, once started, to reach the target as-fast-as-possible, keep the index-finger on the target for about 1 s and then return to the initial position. This was done so as to exclude any reaction-time effect. To be sure that in no way such effect would have affected our results, we automatically excluded those few trials in which the subject recruited the AD within the first 150 ms from the go signal. Throughout the experiment, subjects were instructed to perform the reaching movement by flexing the right shoulder, keeping the elbow, wrist and index-finger extended.

The target consisted in a black diagonal cross (2 x 2 cm) drawn on a flat and rigid white surface. The target position was adjusted for each subject so that the target was at the shoulder height on the subjects' midline, one upper-limb length from their feet.

Figure 1 near here

Experimental design

Subjects memorized the target position by performing several reaching movements, until they felt confident. Thereafter, as sketched in Figure 1, four conditions were studied, in which the subjects had to: 1) look at the floor with the head flexed, then voluntarily gaze and reach the target (*Gaze-Reach*), 2) keep the gaze steadily on the target while reaching it (*Reach in Full Vision*), 3) keep the

head flexed until having touched the target, then gaze at it (*Reach then Gaze*) and 4) look at the floor with the head flexed, then raise the head and eyes to gaze at the target but without moving the arm (*Gaze w/o Reach*). The last condition allowed to separately evaluate the specific postural actions associated to head movements.

Each trial condition was performed in separate blocks consisting of 15 trials each. Every subject performed in random order 7 blocks - 4 *Gaze-Reach* blocks, 1 *Reach in Full Vision* block, 1 *Reach then Gaze* block, 1 *Gaze w/o Reach* block. Subjects had rest for 5 to 10 min between blocks; no subject complained fatigue.

Recordings

In each experiment, electromyographic (EMG) activity, vertical electro-oculogram (EOG-Up, positive when the gaze was directed upward), right arm, right acromion and head kinematics, target position and forces exerted on the ground were synchronously recorded.

EMGs were recorded from the right shoulder flexor Anterior Deltoid (AD) and from two postural muscles of both lower-limbs (Tibialis Anterior, TA and Hamstring, Ham). For each muscle, conventional disposable bipolar electrodes (1 cm diameter) were glued 25mm apart on the skin covering the muscle belly. EMG signals were amplified (1-10 k) and band-pass filtered (30 to 500 Hz).

The EOG-Up was recorded by placing two disposable bipolar electrodes immediately above and below the right eye orbit. The signal was amplified (2 k) and band pass filtered (0.1 to 30 Hz).

A 3D motion analysis system (SMART-D, BTS®; 8 infrared cameras, spatial accuracy better than ± 0.5 mm in all directions) was used to record the arm, acromion and head kinematics as well as the target position. The axes of the 3D reference frame were directed leftward, upward and forward, while its origin was placed on the posterior-right corner of the force platform that recorded the mechanical actions exerted on the ground (AMTI® OR6-7). Reflecting spherical markers (1.5 cm \varnothing) were taped to the right acromion, nasion and inion (secured by elastic band tied around the head. Some reflective tape was applied directly to the distal phalanx of the index-finger to track its position. To identify target position, two hemispherical reflective markers were glued on its flat surface, equidistantly above and below the target cross.

Synchronous data acquisition was accomplished by the SMART-D workstation. EMG and platform signals were A/D converted at a sampling frequency of 1120 Hz, while cameras sampling rate was 70 Hz. EMG, kinematic and force signals were digitalized with 16 bit resolution and stored for offline measurements.

Data analysis

Pre-processing

The EMG traces of the prime mover and those simultaneously recorded from the postural muscles were digitally rectified and integrated (time constant: 10 ms). The index forward movement (Index-Fw) was traced by referring its forward displacement to that of the acromion. Head extension movement was traced as the angle between the nasion-inion segment and the vertical axis. The target position was traced as the mid-position of the segment connecting the two markers on the target board. Force platform data were pre-processed to extract the traces of the three force components exerted on the ground (F-Lw, positive when directed leftward; F-Fw, positive forward; F-Up, positive upward), of the displacement of the centre of pressure (CoP-Lw, CoP-Fw) and of the torque exerted about the vertical axis passing through the CoP (T-Ccw, positive when counter-clockwise).

On *Gaze-Reach*, *Reach in Full Vision* and *Reach then Gaze* movement trials, the onsets of AD EMG were identified by running a mobile window of 1 s over the AD trace. This algorithm searched for those positions in which the samples in the 50 ms following the window were all above or all below the mean value ± 2 SD of the samples within the window. Whenever this criterion was met, the end of the window was taken as an onset. All onsets were visually validated. Movement onset and movement end were respectively identified by applying the same mobile window method to i) the Index-Fw trace and to ii) the forward displacement of the upper marker glued on the target board, that signalled the impact of the index-finger on the target surface. On *Gaze-Reach*, *Reach then Gaze* and *Gaze w/o Reach* trials we also extracted the onset of vertical eye movement and of head extension, by applying the mobile window method to the respective traces.

Classification of Gaze-Reach trials

By comparing the onset timings of AD EMG, vertical eye movement and head extension, the 60 *Gaze-Reach* trials recorded in each subject were classified in two categories: trials in which both the eyes and head movements preceded the AD EMG by at least 5 ms (*Gaze first* condition, 35.0 ± 6.5 % of *Gaze-Reach* trials, mean \pm SEM), and trials in which the eyes and head movements followed the AD EMG by at least the same time (*Reach first*, 35.5 ± 6.6 %). Each subject performed *Gaze first* and *Reach first* trials without following any systematic order. Trials that did not accomplish

one or the other criteria were excluded from the analysis. Among these, in most cases (22.0 ± 4.3 %) the eyes and/or head movements started within ± 5 ms from AD, while in only few cases (7.5 ± 1.2 %) the eyes preceded the AD and the head followed it, or vice-versa.

Measurements

To quantify pointing accuracy and precision in *Gaze first*, *Reach first*, *Reach in Full Vision* and *Reach then Gaze* conditions, for each trial the leftward and upward index-fingertip position with respect to the target were measured at the movement end (horizontal error, positive leftward, and vertical error, positive upward). In each condition, the accuracy in the leftward and upward directions was evaluated by averaging the *signed* values of the respective errors (larger values meaning lower accuracy). Precision was instead evaluated by averaging the *absolute* values of horizontal and vertical errors (larger values meaning lower precision).

In the same movement conditions, we also measured the average 3D coordinates of the index-finger and acromion both in the initial position (from -1 s to -0.5 s prior to AD onset) and at the movement end.

For each experimental condition involving arm movements (*Gaze first*, *Reach first*, *Reach in Full Vision* and *Reach then Gaze*), the traces of EMG, EOG-Up, Index-Fw movement, head extension movement and leftward, upward and forward displacement of the right acromion, as well as the traces of the mechanical actions exerted on the ground were averaged in a fixed temporal window (from -2 to +2 s with respect to AD onset, which became time 0). The onset of postural adjustments was measured on the averaged traces of acromion displacement, EMG and mechanical actions, by applying the same mobile window method used for AD onset. Apart from the leftward acromion displacement (which in many cases started after the onset of index-finger movement and was thus excluded from the analysis, see Results), all these actions always preceded the average onset of index-finger movement, therefore they were classified as APAs. Latency of the APAs was referred to the AD EMG onset, with negative values indicating a time advance. The choice to classify the *Gaze-Reach* trials in the *Gaze first* and *Reach first* categories and to measure the APA onset on the averaged traces, instead of correlating the APA latency to the eye-to-AD or head-to-AD latency in each single trial, stemmed from the need to compensate for the high trial-by-trial variability of the APAs. We directly faced this problem in the data analysis of Caronni et al. (2013), when we had to average at least 5 movement trials in order to get a reliable trace.

Instead, for *Gaze w/o Reach* trial, that do not involve arm movements, the time window for traces averaging was centred on the onset of head extension, which was also taken as reference for

measuring the latencies of the related postural actions, even if they were not anticipatory. Such actions were indeed measured also if they started after the onset of head movement, because the aim of such analysis was to exclude that any “head-induced” action could have affected the onset of APAs measured in *Gaze first* and *Reach first*. Then, we re-referred the latency of APAs in *Gaze first* and *Reach first* with respect to the onset of head extension and compared the results with the latency of the head-induced postural actions in *Gaze w/o Reach*. This procedure allowed to verify that the APAs always started before the postural actions associated with head movements, as explained in the Results section and in Figure 5.

Statistical analysis

As explained in the Introduction, i) in *Gaze first* trials the subjects were expected to get visual information about target position prior to starting the arm movement, while in *Reach first* trials that information was postponed; ii) in *Reach in Full Vision* there was full availability of visual information prior to arm movement while in *Reach then Gaze* the opposite occurred, but in both cases the eyes and head were still throughout the arm movement. Such design contains two independent factors: i) the availability of visual information prior to arm movement (VIEW, present in *Gaze first* and *Reach in Full Vision* while absent in *Reach first* and *Reach then Gaze*), and ii) the presence of head and eyes movements in concomitance with arm movements (HEAD, present in *Gaze first* and *Reach first* while absent in *Reach in Full Vision* and *Reach then Gaze*).

Therefore, two-way (VIEW x HEAD) repeated-measures ANOVAs were used to compare across conditions the latency, duration and amplitude of Index-Fw movement. With regard to the latency of APAs in upward and forward acromion displacement, in postural muscles and in mechanical actions on the ground, a third factor, the *Kinematic, Electromyographic and Mechanical Postural Parameters* (KEMPP) was added, with one level for each kinematics, muscular and mechanical trace, thus giving a three-way ANOVA. Given that the muscular activities are the cause of the body segments’ displacement and of the mechanical actions on the ground, the main effect of KEMPP should be considered of marginal interest, since it would simply reflect the time difference between a cause and its effect. However, the interactions within the same ANOVA allowed to evaluate any possible modification of the effect(s) of HEAD and/or VIEW among the different postural recordings. Three-way ANOVAs (VIEW x HEAD x DIRECTION) were applied to compare across conditions i) the mean signed values of the horizontal and vertical errors, ii) the mean absolute values of the horizontal and vertical errors, iii) the average 3D coordinates of the index-fingertip in the initial position, iv) the average index-fingertip coordinates at movement end,

v) the average 3D coordinates of the acromion in the initial position, vi) the average acromion coordinates at movement end.

For those ANOVA factors with more than two levels, Mauchley's test was applied to assess sphericity violation, in which case the degrees of freedom (df) were adjusted according to the Greenhouse-Geisser method. Tukey post-hoc tests were applied to dissect significant effects. In all tests, significance threshold was set at $p = 0.05$.

Results

Coordination strategies in Gaze-Reach movements

When subjects were asked to coordinate eyes, head and arm movements so as to *Gaze-Reach* the target as fast as possible, two coordination strategies could be discriminated: in some trials, both the eyes and head movements preceded the arm prime mover activity (*Gaze first*), while in other trials the opposite occurred (*Reach first*). Figure 2 illustrates the averaged traces of *Gaze first* and *Reach first* trials in a representative subject (black and white lines, respectively), time-locked on the recruitment of the shoulder flexor AD. Note that in both conditions APAs were observed in the upward and forward displacement of the right acromion (Ac-Up and Ac-Fw), in leg muscles (TA and Ham) and in the mechanical actions exerted on the ground (CoP-Lw, CoP-Fw, F-Lw, F-Fw, F-Up, T-Ccw). Despite focal movement kinematics were similar in the two conditions (Index-Fw, right uppermost panel), it is evident that APAs in leg muscles were more anticipated in *Gaze first* than in *Reach first*. This result was paralleled by the Ac-Up and Ac-Fw traces and by the mechanical actions on the ground, as apparent in CoP-Lw and T-Ccw. With regard to the leftward displacement of the acromion (Ac-Lw), its trace showed a positive deflection in all subjects which, however, started after the Index-Fw movement in four of them, so that such deflection could not be classified as APA. Therefore, the Ac-Lw trace was excluded from the analysis.

Figure 2 near here

Changes in APA latencies in the different reaching movements

In the whole population, the average latency of vertical eye movement (EOG-Up) with respect to AD onset was -102.7 ± 12.8 ms in *Gaze first* vs. 26.5 ± 5.1 ms in *Reach first*, while values for the latency of Head extension in the respective conditions were -40.5 ± 8.4 ms vs. 33.0 ± 4.6 ms.

Latencies of APAs measured in muscular and mechanical traces with respect to AD onset are shown in Figure 3 for the whole population. Besides values obtained in *Gaze first* and *Reach first*, the figure also illustrates values pertaining to the two control conditions *Reach in Full Vision* and *Reach then Gaze*. The latter two conditions were introduced to evaluate the contribution of the head movement on APAs both in presence and in absence of visual information. The APAs in acromion kinematics, leg muscles and forces on the ground were more anticipated in *Gaze first* than in *Reach first*. This is particularly evident in right Ac-Fw (-72.4 ± 12.1 ms vs. -21.7 ± 12.4 ms), right TA (-93.6 ± 27.2 ms vs. -39.3 ± 26.7 ms) and Ham (-103.4 ± 16.5 ms vs. -54.0 ± 10.7 ms), as well as in CoP-Lw (-17.7 ± 19.4 ms vs. 13.9 ± 20.3 ms), CoP-Fw (-72.9 ± 29.8 ms vs. 4.8 ± 31.4 ms) and F-Fw (-106.7 ± 22.9 ms vs. -55.3 ± 24.8 ms). This was also true when comparing *Reach in Full Vision* and *Reach then Gaze* (right Ac-Fw: -63.4 ± 14.1 ms vs. -26.2 ± 18.7 ms; right TA: -80.9 ± 30.8 ms vs. -34.4 ± 33.7 ms; right Ham: -105.4 ± 23.7 ms vs. -33.5 ± 40.4 ms; CoP-Lw: -26.7 ± 28.9 ms vs. 23.7 ± 23.2 ms; CoP-Fw: -57.1 ± 27.0 ms vs. 13.3 ± 28.8 ms and F-Fw: -101.7 ± 30.1 ms vs. -59.5 ± 27.7 ms). Note that in both comparisons, APAs were anticipated when visual information was present before starting arm movements (*Gaze first* and *Reach in Full Vision*). Figure 3d plots the grand-average of APA latencies (Pooled APAs), which illustrates that the time lag from *Gaze-* to *Reach first* was comparable to that measured between *Reach in Full Vision* and *Reach then Gaze* (44.3 ± 8.9 ms vs. 39.5 ± 7.9 ms). It is also worth noting that the latency of eye movements in *Gaze first* was very close to the latencies of the more anticipated APAs (right TA, right Ham and F-Fw), moreover it was not statistically different (paired t-test $p = 0.125$) from the latency of the earliest APA (T-Ccw: -129.9 ± 17.7 ms). Finally, figure 3a reports that, as in the representative subject, the average kinematic parameters of the index-finger displacement were similar in the four conditions (in average, latency from AD onset 97 ms, movement duration 325 ms and amplitude 629 mm).

Statistical comparison on APA latencies was performed by a three-way ANOVA, which included the two independent factors distinguishing the four conditions, i.e. VIEW (*Gaze first* and *Reach in Full Vision* vs. *Reach first* and *Reach then Gaze*) and HEAD (*Gaze first* and *Reach first* vs. *Reach in Full Vision* and *Reach then Gaze*) as well as a third factor, KEMPP, accounting for the different APAs (Ac-Up vs. Ac-Fw vs. right TA vs. ... T-Ccw). Apart from the main effect of KEMPP ($p = 0.0017$), which is of marginal interest (as explained in Methods), this ANOVA test

only disclosed a main effect of VIEW ($p = 0.0003$). The main effect of HEAD and all interactions were instead not significant (see Table 1). This witnesses that the time-shift induced by the availability of visual information (effect of VIEW) was similar in all traces.

The similarity of focal movement kinematics was instead confirmed by three separate two-way ANOVAs with factors VIEW and HEAD, run on latency, duration and amplitude of the index-finger forward displacement. Indeed, ANOVAs did not find any main effect of VIEW or HEAD, nor interactions (see Table 1).

The similarity of focal movement kinematics is also witnessed by the fact that the average 3D coordinates of the index-finger and acromion did not change among conditions, both in the initial position and at the end of the reaching movement (see Table 2).

Figure 3 near here

Accuracy and precision of the different reaching movements

The top left panel of Figure 4 shows, in the representative subject, the horizontal and vertical pointing error, i.e. the end position of the index-fingertip with respect to the target. Note that the clouds referring to each condition are almost superimposed and centred on the target, but the scatter looks somewhat larger in *Reach then Gaze* than in the other conditions, especially in the vertical direction. The mean *signed* pointing error (\pm SEM) in the whole population is plotted in the bottom left panel. This parameter was similar among all conditions (Horizontal error: -3.7 ± 1.3 mm in *Gaze first*, -5.3 ± 1.2 mm in *Reach first*, -5.7 ± 0.9 mm in *Reach in Full Vision* and -7.1 ± 1.7 mm in *Reach then Gaze*; Vertical error: -3.4 ± 2.5 mm in *Gaze first*, 1.9 ± 1.3 mm in *Reach first*, -3.0 ± 1.8 mm in *Reach in Full Vision* and 1.9 ± 4.4 mm in *Reach then Gaze*), indicating no changes in movement *accuracy* and again witnessing the similarity of focal movement kinematics. Indeed, a three-way ANOVA with factors VIEW x HEAD x DIRECTION (horizontal vs. vertical) only found a main effect of DIRECTION ($p = 0.0428$) while all other main effects and interactions did not reach significance (see Table 1).

The horizontal and vertical bar charts illustrate the mean *absolute* error in the whole population. Such parameters were larger, i.e. *precision* was lower, in *Reach then Gaze* (Horizontal error: 16.1 ± 2.4 mm; Vertical error: 24.8 ± 1.8 mm) with respect to the other three conditions, without significant differences among them (Horizontal error: 8.5 ± 0.9 mm in *Gaze first*, 10.0 ± 1.1 mm in *Reach first* and 10.2 ± 0.9 mm in *Reach in Full Vision*; Vertical error: 15.1 ± 1.9 mm in *Gaze first*, 12.9 ± 0.9 mm in *Reach first* and 14.4 ± 1.5 mm in *Reach in Full Vision*). Indeed the

three-way ANOVA found significant main effects for all factors (VIEW $p = 0.0039$, HEAD $p = 0.0081$, DIRECTION $p < 0.0001$, see Table 1) and significant interactions VIEW x HEAD ($p = 0.0034$) and VIEW x HEAD x DIRECTION ($p = 0.0392$, for Tukey post-hoc see asterisks in Fig. 4), the other interactions being not significant.

Figure 4 near here

Postural actions associated to head movements

In the *Gaze w/o Reach* condition, subjects had to raise the head and look at the target, but without moving the arm. This allowed to separately evaluate the specific postural actions - not necessarily anticipatory - associated to head movements. Average traces, time-locked to the onset of head extension, are plotted for the representative subject in Figure 5, together with the traces of *Gaze first* and *Reach first* movements, time-locked to the respective head extension onset; therefore, the thin vertical dashed line marks the onset of head extension in *Gaze w/o Reach*, *Gaze first* and *Reach first*. Head movements apparently induced appreciable postural action only in Ac-Up, Ac-Fw, F-Fw and F-Up, but such head-induced actions started after the APAs of *Gaze first* and *Reach first*.

Analysis of the whole population data found that head-induced postural actions were present in Ac-Fw, F-Fw and F-Up of all 10 subjects, in Ac-Up of 8 subjects and in CoP-Fw of 6 of them, but in all cases such postural actions started after the APAs of *Gaze first* and *Reach first*. Thus, the head extension alone could not affect the onset and the early phase of the APAs development.

Figure 5 near here

Discussion

This study demonstrates that, when reaching a target of known position, the APA latency depends on the moment at which the CNS expects that visual information about the target will be available. Indeed APAs were more anticipated in *Gaze first* and *Reach in Full Vision* (with no time difference among the two) with respect to *Reach first* and *Reach then Gaze* (again with no time difference between the two). The observation that the latency of eye movements in *Gaze first* was similar to that of the earliest APAs strongly suggests that in this condition the motor plan includes the request

for visual information, so that the commands to eyes and postural muscles are built-up at the same time. Instead, in *Reach first* the request for visual information seems de-coupled, and in any case delayed, with respect to the motor action. This means that in the first situation the CNS knows that visual information will be already available when the hand will start to move, as in *Reach in Full Vision*, while the second case seems more similar to the *Reach then Gaze* condition, where vision availability is seemingly not required by the CNS. Finally, the change in APA latency observed when changing the timing of eye-head movements with respect to arm recruitment, i.e. in *Gaze first* vs. *Reach first*, indirectly suggests a correlation between APA and eye-head timings, though a direct intra-subject correlation could not be drawn because of the high trial-by-trial trace variability (see Methods). We also searched, without success, for an inter-subject correlation between the mean APA latencies and the corresponding eye movement latency. Such lack of significance, however, does not preclude that an intra-subject correlation did occur.

It is somehow difficult to match our results with comparable studies on APAs and vision, because literature on this topic is scarce. First of all, our results are in agreement with those obtained by Krigolson et al. (2012), who showed different cortical motor potentials in visually-guided reaching with respect to memory-guided reaching, suggesting a different movement planning in the two conditions. Our data are also in accordance with the proposal of Gopal and Murthy (2015), that the oculomotor control is not independent from the control of body segments orientation during the execution of a voluntary movement, as well as with the results of Reed-Jones et al. (2009), who illustrated that the changes in orientation of head, trunk, and pelvis when stepping around a corner occurred at different timings when accomplishing the task either in a “free-gaze” or in a “fixed-gaze” condition. In this last study, the subjects oriented the body segments prior to the arrival at the corner when the eyes were free to move, while they rotated the head, trunk, and pelvis segments only after the corner in the fixed-gaze condition. Thus, “the eye movement itself is generated as part of a coordinated eye, head, and body rotation” (Reed-Jones et al. 2009) and according to our results this statement should include also the APA control. Finally, our results are in agreement with those of Lin and Yang (2011), who illustrated that APAs in step initiation were earlier when performed with open eyes than with closed eyes, a finding very similar with our observation of more anticipated APAs in *Reach in Full Vision* with respect to *Reach then Gaze*. Considering also our *Gaze first* and *Reach first* data, the expectancy of visual information may have played a role also in Lin and Yang experiments.

A criticism to the present work might be that the observed modifications in APA latency were simply a consequence of the different timings of the head extension between *Gaze first* and *Reach first*. However, in order to exclude such a bias, an experimental session was specifically

designed in which subjects moved only head and eyes (*Gaze w/o Reach*). In these trials “head-induced” postural actions were systematically observed in CoP-Fw, F-Fw and F-Up, but the absence of postural changes in TA and Ham suggests that those mechanical actions should be ascribed to the activation of other muscles, possibly not involved in the postural control of arm reaching movements. Moreover, the fact that in all subjects the “head-induced” actions always followed the onset of APAs recorded in *Gaze first* and *Reach first* ruled-out the timing of head extension as a possible bias factor.

There are two other factors that are known to influence the APAs. First, APAs are tuned depending on the postural demand caused by the focal movement (Horak et al. 1984; Lee et al. 1987; Aruin and Shiratori 2004; Shiratori and Aruin 2007; see Bouisset and Do 2008 for a review), but the similarity of mean amplitude, duration and latency of the index-finger movement in the different conditions clearly ruled-out also this bias. Second, it has been recently demonstrated that APA latency changes according to the intended speed of the movement (*e.g.* “go-fast” vs. “go-slow” instruction), not to the actual movement velocity (Esposti et al. 2015). Considering that in our experiments the subjects had to perform the pointing movement “as-fast-as-possible” in all conditions, this should not have affected our results.

Visual feedback and movement accuracy

Indeed, also another important kinematic parameter did not change, *i.e.* the average index-fingertip end position (see Fig. 4). On one hand, taking into account the differences in APA timing, this witnesses that there were some kind of mechanical compensation, *e.g.* permitted by changes in APA amplitude and/or in consecutive postural adjustments. However, these parameters were not considered in the present paper because they could have been biased by the postural adjustments linked to the head movements. On the other hand, it is important to consider that in *Reach then Gaze* the target was not visible until the movement end, so that the subject could not rely on visual feedback for online corrections, which instead could likely occur in *Reach in Full Vision* and *Gaze first*, and could not be excluded in *Reach first*. Consequently, the similarity of the average end position of the index-finger in *Reach then Gaze* with respect to the other conditions witnesses that the visuospatial memory of the target, adequately refreshed after each movement, was sufficient to reach the same *accuracy*. Therefore, the contribution of visual feedback to movement accuracy was likely negligible in *Reach in Full Vision*, as well as in *Gaze first* and *Reach first*, two conditions in which the visuospatial memory was updated well before the movement end. In this regard, Gonzalez et al. (2012) demonstrated that when playing golf, there were similar constant errors (*i.e.*

accuracy) in the direction of the putt toward a 3 m target, under full vision, no vision, target focus and ball focus. Moreover, an indirect support to the above conclusion might also come from Ypsilanti et al. (2009), who reported that in arm reaching movements there were no differences in aiming performance when looking at the target with binocular vs. monocular vision, either dominant or non-dominant. Nevertheless, we observed a significant APA delay in *Reach first* and *Reach then Gaze* vs. *Gaze first* and *Reach in Full Vision*, indicating that even if the CNS can program an accurate movement basing only on visuospatial memory, it takes into account the moment at which visual information about target position is expected to become available.

Visual feedback and movement precision

As stated above, in all conditions the average end position of the index-fingertip with respect to the target did not change, giving similar mean signed errors. Instead, in *Reach then Gaze* the mean absolute error was larger than in the other conditions, as the finger end positions were more scattered (Fig. 4). Altogether, these data suggest that online visual feedback, despite not strictly required for getting movement accuracy, was actually exploited for getting movement *precision*. While this was self-evident in *Reach in Full Vision* movements, in *Gaze first* and *Reach first* this result may be explained by two non-mutually exclusive possibilities. The first is that the eyes acquired the target before the index-finger reached it, thus actually providing visual feed-back for online corrections. This possibility would be in accordance with Heath's proposal (2005) that the target representation stored in memory can be combined with vision of the moving limb for the online control of memory-guided reaches. This most likely occurred in *Gaze first*, but it cannot be excluded in *Reach first*. The second possibility is that the "outflow" signal associated with eye orientation toward the target could have *per-se* improved movement performance, as observed by Enright (1995) and by Hollands and Marple-Horvat (1996). In this regard, the strict relationship between eye rotation and movement outcome was also highlighted by observing that coordinating the eye movements with the steering increased performance on a driving simulation, even if half of the simulator screen was obscured so that such eye movements could not get any visual information (Wilson et al. 2007). This possibility may have been exploited in both *Gaze first* and *Reach first*. Independently of the specific approach, the conclusion to be envisaged is that visuospatial memory plays a key role in movement *accuracy*, while online visual information and eye movements proprioception, i.e. "active vision", seem to be engaged in movement *precision*.

Conclusions

According to the chosen strategy, *Gaze-Reach* movements are programmed by taking into account whether online visual information about target position is expected to become available. In fact, when *Gazing first*, the CNS takes into account that such information is already available when approaching the target, like in *Reach in Full Vision*, which actually is a visually-guided reaching. Instead, when *Reaching first*, the CNS does not rely on such information, like in *Reach then Gaze*, which actually is a sort of blind reaching. Neither the ocular movements nor the head extension seem to be responsible for the change in the APA programming, given the similarity of the *Gaze first* to *Reach first* and the *Reach in Full Vision* to *Reach then Gaze* time-lags. Thus, it is likely that the availability of visual information influences the postural control of voluntary arm movements.

Finally, considering that the cerebellum plays a crucial role in eye-head-hand coordination during tracking movements (Miall et al. 2001) and that it is also involved in properly timing the anticipatory postural adjustments (Bruttini et al. 2015), it would be of interest to apply the present experimental protocol to ataxic patients, in order to evaluate how the availability of visual information would modify the APA timing and also how the time relations between eyes, head and arm movements would be affected.

Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

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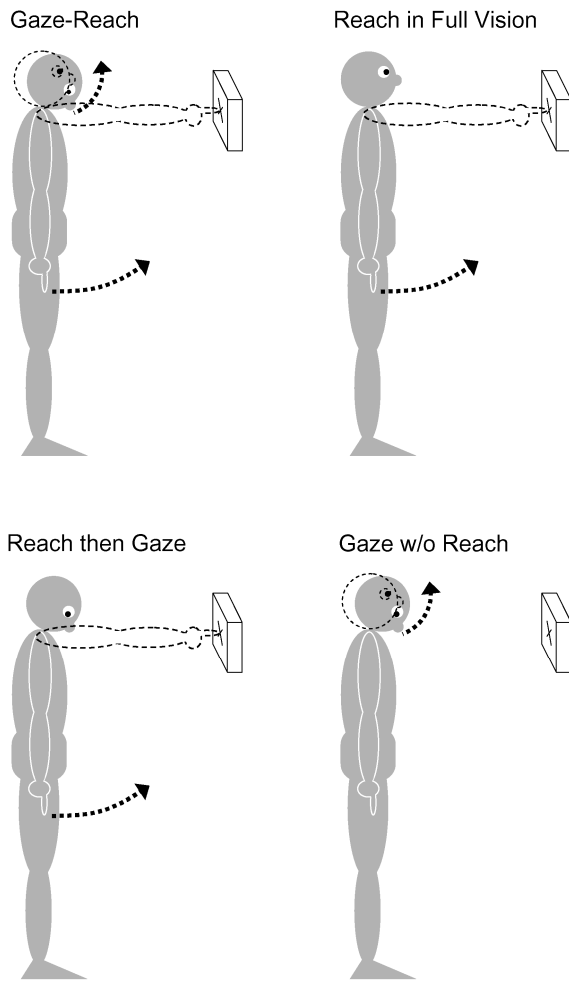


Fig. 1 Experimental paradigm. Subjects standing on a force platform had to reach with the index-fingertip a target placed at shoulders height on the subject's midline. The elbow, wrist and index-finger were kept extended. Four conditions were studied. *Gaze-Reach*: starting by looking at the floor, subjects had to move the eyes, head and arm so as to reach the target with both gaze and index-finger. *Reach in Full Vision*: looking at the target, subjects had to reach it. *Reach then Gaze*: subjects had to keep the gaze at the floor until having touched the target. *Gaze w/o Reach*: subjects had to move only head and eyes to gaze the target, without reaching it. Dotted arrows indicate head and arm movements, whose final position is outlined by dashed contours.

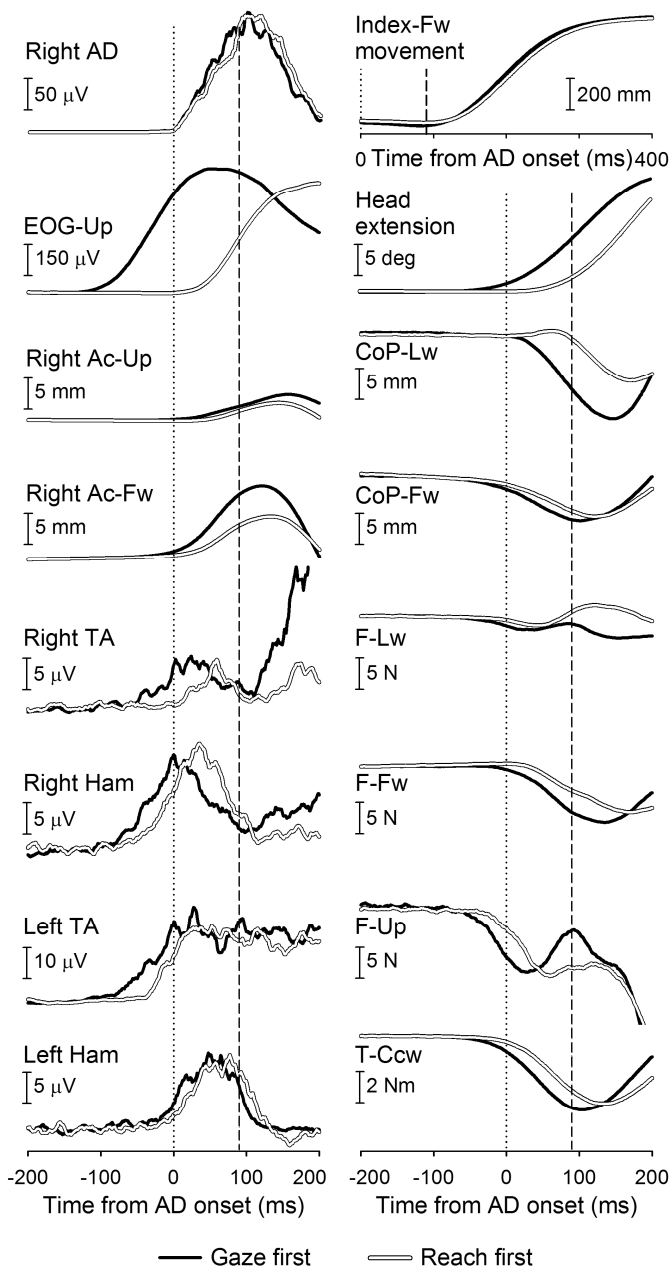


Fig. 2 *Gaze-Reach* movements in one representative subject. Trials fell in two categories: *Gaze first* (black traces), in which both the eyes (EOG-Up) and head movements (Head extension) preceded the EMG onset in the prime mover (right Anterior Deltoid, AD) and *Reach first* (white traces), in which the opposite occurred. The average recordings of *Gaze first* and *Reach first* trials are time-locked to the onset of AD EMG (0 ms, dotted vertical line). On the left panel, the AD EMG and the EOG-Up traces are followed by the upward and forward displacement of the right acromion (Ac-Up and Ac-Fw), as well as by the rectified and integrated EMG from Tibialis Anterior (TA) and Hamstring (Ham) of right and left body sides. On the right panel, the forward displacement of the index-fingertip (Index-Fw movement) is followed by the Head extension trace and by the force platform recordings: the displacement of the Centre of Pressure (CoP-Lw, positive when directed leftward and CoP-Fw, positive forward), the three components of the force exerted on the ground (F-Lw; F-Fw; F-Up, positive upward) and the torque about the vertical axis passing through the CoP (T-Ccw, positive when counter-clockwise). Vertical dashed lines mark the onset of the Index-Fw movement.

Despite the Index-Fw movement had similar kinematics in the two conditions, APAs in right acromion displacement and in TA and Ham of both sides occurred earlier in *Gaze first* than in *Reach first*, as it also happened for the resulting APAs in the mechanical actions exerted on the ground.

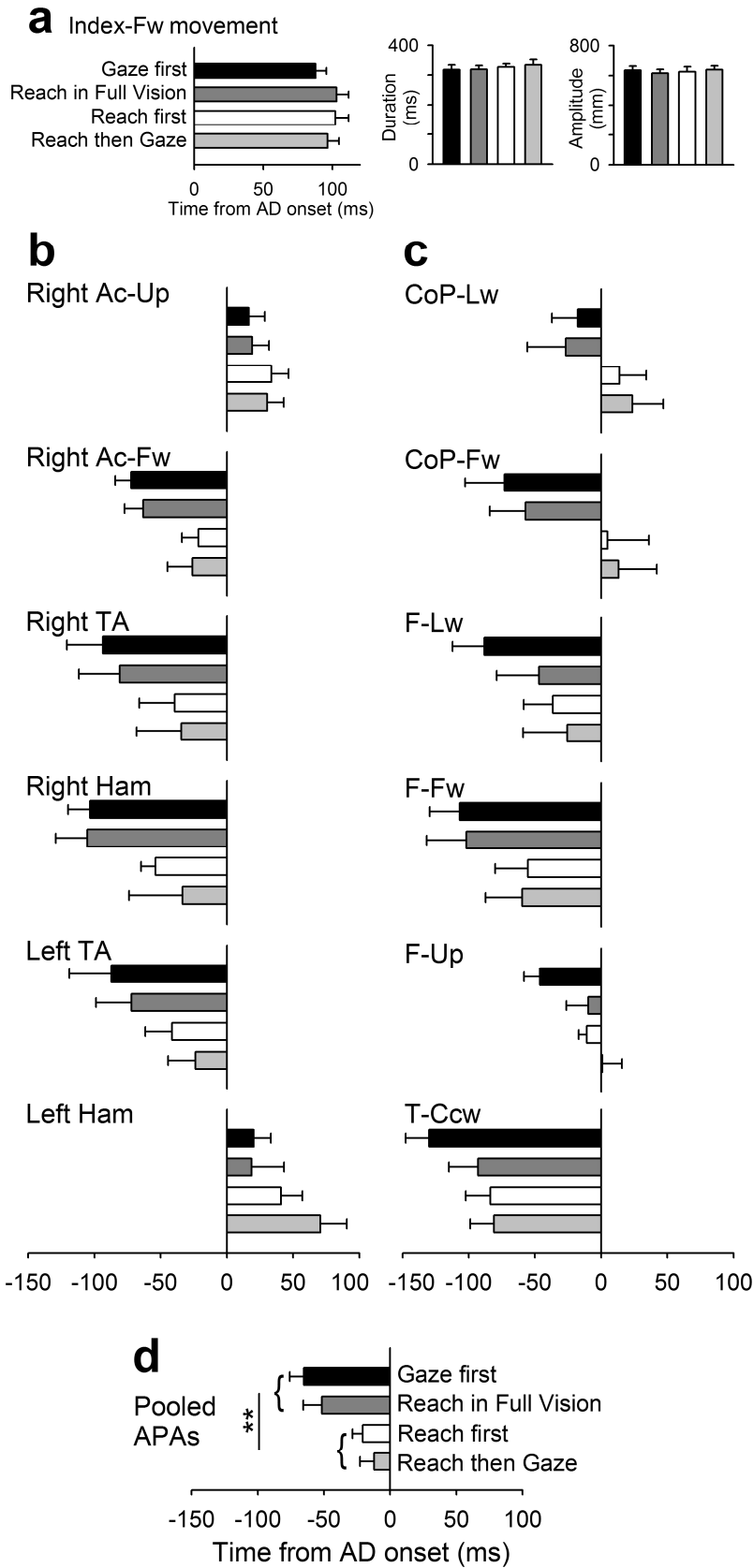


Fig. 3 Mean latency, duration and amplitude of the index-fingertip movement (Index-Fw) did not change across the four conditions (a). Instead, APA onsets in Acromion displacement (Ac-Up and Ac-Fw, b), in Tibialis Anterior and Hamstring muscles (TA and Ham, b), in Centre of Pressure (CoP-Lw and CoP-Fw, c), in force components on the ground (F-Lw, F-Fw, F-Up, c) as well as in torque about the vertical axis (T-Ccw, c) were more anticipated in *Gaze first* and *Reach in Full Vision* (black and dark grey), than in *Reach first* and *Reach then Gaze* (white and light grey). This is highlighted in panel (d), which illustrates the latencies obtained after pooling all APAs in each condition as well as the results of the statistical analysis (** $p = 0.0003$). Mean values from all subjects (\pm SEM); latencies referred to onset of Anterior Deltoid (AD).

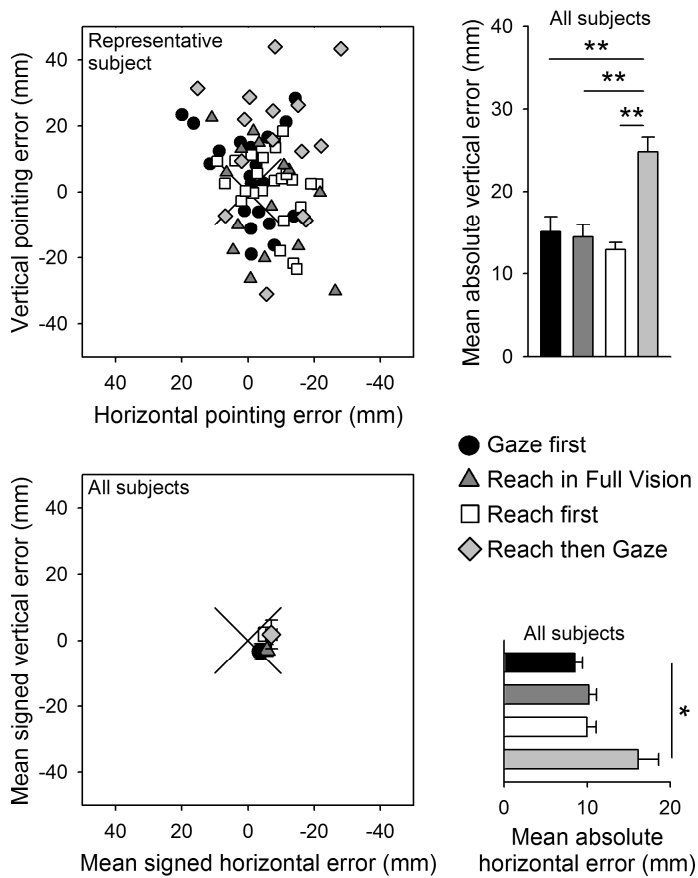


Fig. 4 Accuracy and Precision of the reaching movements. The top left panel shows the horizontal and vertical pointing errors in the representative subject at the end of the *Gaze first* (black), *Reach in Full Vision* (dark grey), *Reach first* (white) and *Reach then Gaze* (light grey) movements. The black cross marks the centre of the target. The bottom left panel reports the mean signed values (\pm SEM) in the whole population. Statistics did not find any significant difference among the four conditions. On the right side, the vertical and horizontal bar charts illustrate the mean absolute values of pointing error in the respective direction. Statistics found a higher absolute error in *Reach then Gaze* than in the other conditions, as marked by asterisks (* $p < 0.05$; ** $p < 0.005$).

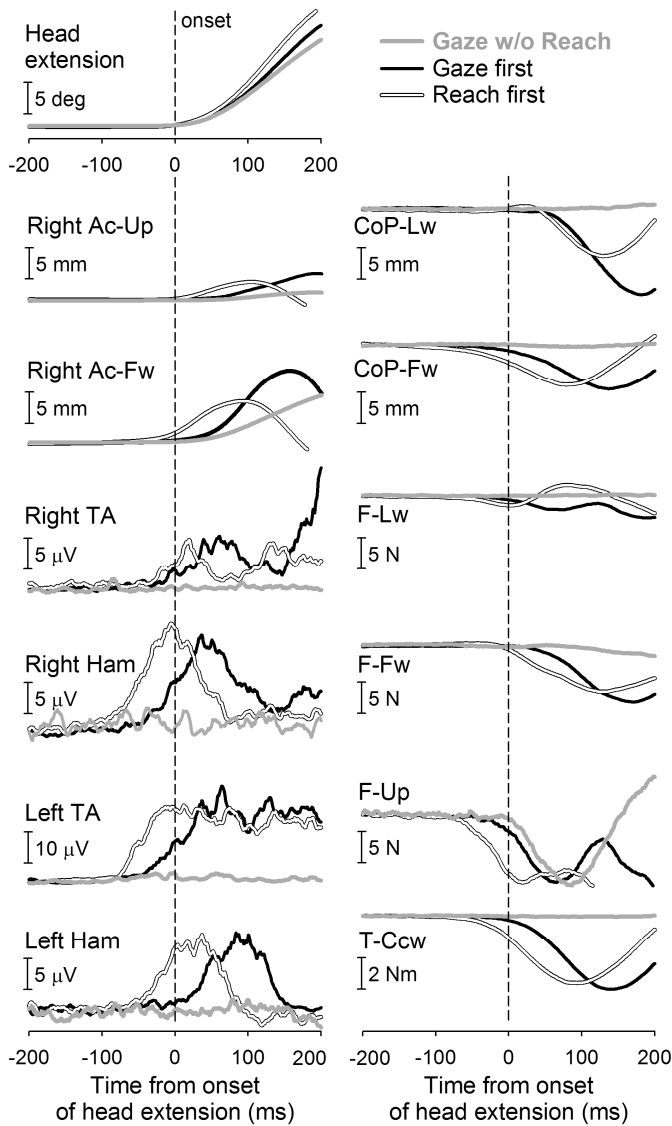


Fig. 5 Traces from *Gaze w/o Reach* movements (grey), compared with traces from *Gaze first* (black) and *Reach first* (white) movements. Same representative subject of figure 2. Please note that the average recordings are time-locked to the onset of head extension (vertical dashed lines, 0 ms). On the left, from top to bottom, goniometric recordings of the head extension, upward and forward displacement of the right acromion (Ac-Up and Ac-Fw) and rectified and integrated EMG from Tibialis Anterior (TA) and Hamstring muscles (Ham). On the right, the force platform recordings (Centre of Pressure, CoP-Lw and CoP-Fw; Force components, F-Lw, F-Fw, F-Up; Torque about the vertical axis, T-Ccw). Note that head movements induced appreciable postural action only in Ac-Up, Ac-Fw, F-Fw and F-Up. It is however apparent that the head-induced postural actions started after the APAs of *Gaze first* and *Reach first*.

Table 1 Results of repeated measures ANOVAs on: *APA Latency* recorded in the acromion displacement, in the different muscles and in the mechanical actions on the ground; *Index-Fw movement* latency, duration and amplitude; *Mean Signed Error* and *Mean Absolute Error* in the horizontal and vertical directions. ANOVA factors were: VIEW (V), HEAD (H), KEMPP (K), DIRECTION (D); see Methods for details. In case of sphericity violation, the degrees of freedom (df 1,2) were adjusted according to the Greenhouse-Geisser method.

| | | <i>F</i> | df 1, 2 | <i>p</i> | | | <i>F</i> | df 1, 2 | <i>p</i> | |
|-------------------|-----------|----------|-----------|----------|-------------------|---------------------|----------|---------|----------|---------|
| APA Latency | V | 32.94 | 1, 9 | 0.0003 | Mean Signed Error | V | 2.80 | 1, 9 | 0.13 | |
| | H | 1.66 | 1, 9 | 0.23 | | H | 0.37 | 1, 9 | 0.56 | |
| | K | 5.82 | 3.5, 32.0 | 0.0017 | | D | 5.56 | 1, 9 | 0.0428 | |
| | VxH | 0.33 | 1, 9 | 0.58 | | VxH | 0.002 | 1, 9 | 0.96 | |
| | VxK | 1.42 | 3.6, 32.1 | 0.25 | | VxD | 4.62 | 1, 9 | 0.06 | |
| | HxK | 0.39 | 3.4, 30.8 | 0.78 | | HxD | 0.52 | 1, 9 | 0.49 | |
| | VxHxK | 0.65 | 4.5, 40.3 | 0.64 | | VxHxD | 0.016 | 1, 9 | 0.90 | |
| Index-Fw Movement | latency | V | 0.58 | 1, 9 | 0.46 | Mean Absolute Error | V | 14.76 | 1, 9 | 0.0039 |
| | | H | 0.56 | 1, 9 | 0.47 | | H | 11.42 | 1, 9 | 0.0081 |
| | | VxH | 3.51 | 1, 9 | 0.09 | | D | 62.45 | 1, 9 | <0.0001 |
| | duration | V | 1.65 | 1, 9 | 0.23 | | VxH | 15.57 | 1, 9 | 0.0034 |
| | | H | 0.19 | 1, 9 | 0.67 | | VxD | 0.07 | 1, 9 | 0.79 |
| | | VxH | 0.07 | 1, 9 | 0.80 | | HxD | 1.02 | 1, 9 | 0.34 |
| | amplitude | V | 0.73 | 1, 9 | 0.41 | | VxHxD | 5.81 | 1, 9 | 0.0392 |
| | | H | 0.15 | 1, 9 | 0.70 | | | | | |
| | | VxH | 4.21 | 1, 9 | 0.07 | | | | | |

Table 2 3D coordinates of the index-fingertip and of the acromion measured both in the initial position and at the end of the reaching movement, in the four conditions. Mean values \pm SEM, measured from the posterior right corner of the force platform, taken as the origin of the 3D reference frame. Repeated measures ANOVAs with factors VIEW (V), HEAD (H) and DIRECTION (D) did not found any significant main effect of VIEW or HEAD or any interaction, witnessing the similarity of movement kinematics across conditions. In case of sphericity violation, the degrees of freedom (df 1,2) were adjusted according to the Greenhouse-Geisser method.

| | movement condition | direction | | | three-way repeated-measures ANOVA | | | | | |
|-------------------------------------|-----------------------|-------------|--------------|---------------|-----------------------------------|-----------|----------|------------|-----------|----------|
| | | leftward | forward | upward | <i>F</i> | df 1, 2 | <i>p</i> | <i>F</i> | df 1, 2 | <i>p</i> |
| index-fingertip initial pos (mm) | Gaze first | 17 \pm 12 | 320 \pm 15 | 716 \pm 15 | V 2.32 | 1, 9 | 0.16 | VxH 2.34 | 1, 9 | 0.16 |
| | Reach in Full Vision | 17 \pm 15 | 336 \pm 14 | 717 \pm 15 | H 0.04 | 1, 9 | 0.84 | VxD 0.85 | 1.3, 11.8 | 0.40 |
| | Reach first | 15 \pm 13 | 322 \pm 15 | 718 \pm 15 | D 563 | 2, 18 | <0.0001 | HxD 1.33 | 1.2, 10.8 | 0.28 |
| | Reach then Gaze | 10 \pm 14 | 320 \pm 17 | 713 \pm 15 | | | | VxHxD 0.88 | 1.1, 10.2 | 0.38 |
| index-fingertip final pos (mm) | Gaze first | 227 \pm 9 | 991 \pm 16 | 1462 \pm 19 | V 1.93 | 1, 9 | 0.20 | VxH .002 | 1, 9 | 0.96 |
| | Reach in Full Vision | 225 \pm 9 | 992 \pm 15 | 1463 \pm 19 | H 0.08 | 1, 9 | 0.78 | VxD 2.77 | 1.2, 10.4 | 0.12 |
| | Reach first | 226 \pm 9 | 992 \pm 15 | 1468 \pm 19 | D 1736 | 2, 18 | <0.0001 | HxD 0.77 | 1.1, 10.3 | 0.42 |
| | Reach then Gaze | 222 \pm 9 | 991 \pm 15 | 1471 \pm 18 | | | | VxHxD 0.20 | 2, 18 | 0.82 |
| acromion initial pos (mm) | Gaze first | 64 \pm 5 | 220 \pm 8 | 1487 \pm 26 | V 2.71 | 1, 9 | 0.13 | VxH 3.43 | 1, 9 | 0.10 |
| | Reach in Full Vision | 60 \pm 6 | 221 \pm 7 | 1486 \pm 26 | H 0.31 | 1, 9 | 0.59 | VxD 0.14 | 2, 18 | 0.87 |
| | Reach first | 65 \pm 5 | 218 \pm 8 | 1488 \pm 26 | D 2067 | 1.2, 10.7 | <0.0001 | HxD 2.35 | 1.1, 9.8 | 0.16 |
| | Reach then Gaze | 65 \pm 5 | 226 \pm 8 | 1487 \pm 26 | | | | VxHxD 1.44 | 2, 18 | 0.26 |
| acromion final pos (mm) | Gaze first | 91 \pm 7 | 270 \pm 13 | 1516 \pm 27 | V 0.91 | 1, 9 | 0.36 | VxH 0.04 | 1, 9 | 0.85 |
| | Reach in Full Vision | 89 \pm 7 | 268 \pm 13 | 1517 \pm 28 | H 1.57 | 1, 9 | 0.24 | VxD 1.50 | 2, 18 | 0.25 |
| | Reach first | 92 \pm 7 | 269 \pm 13 | 1518 \pm 28 | D 1580 | 1.2, 10.8 | <0.0001 | HxD 0.92 | 1.3, 11.5 | 0.38 |
| | Reach then Gaze | 90 \pm 8 | 273 \pm 12 | 1513 \pm 28 | | | | VxHxD 3.06 | 1.2, 11.3 | 0.10 |