Visual and non-visual control of landing movements in humans

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1. The role of vision in controlling leg muscle activation in landing from a drop was investigated. Subjects (n = 8) performed 10 drops from four heights (0.2, 0.4, 0.6 and 0.8 m) with and without vision. Drop height was maintained constant throughout each block of trials to allow adaptation. The aim of the study was to assess the extent to which proprioceptive and vestibular information could substitute for the lack of vision in adapting landing movements to different heights.

2. At the final stages of the movement, subjects experienced similar peak centre of body mass (CM) displacements and joint rotations, regardless of the availability of vision. This implies that subjects were able to adapt the control of landing to different heights. The amplitude and timing of electromyographic signals from the leg muscles scaled to drop height in a similar fashion with and without vision.

3. However, variables measured throughout the execution of the movement indicated important differences. Without vision, landings were characterised by 10% larger ground reaction forces, 10% smaller knee joint rotations, different time lags between peak joint rotations, and more variable ground reaction forces and times to peak CM displacement.

4. We conclude that non-visual sensory information (a) could not fully compensate for the lack of continuous visual feedback and (b) this non-visual information was used to reorganise the motor output. These results suggest that vision is important for the very accurate timing of muscle activity onset and the kinematics of landing.
vestibular information could substitute fully for the lack of vision in adapting landing movements to different heights. To distinguish between these two alternatives, the subjects' performance was assessed by measuring the kinematics of the movements as well as the vertical ground reaction force ($F_z$) produced after foot contact. We also measured the EMG activity from four leg muscles to determine the extent to which the removal of vision affected the modulation of EMG timing and amplitude to drop height. Our expectation was that in the absence of vision, the skill would degrade. Hence, landings without continuous visual feedback would be characterised by distinguishable patterns of EMG and kinematic adaptation to drop heights.

**METHODS**

**Protocol**

Eight subjects were asked to land on a force platform from drops of 0.2, 0.4, 0.6 and 0.8 m under two experimental conditions: without vision (experiment 1) and with vision (experiment 2). All of the subjects (seven males and one female) were physically active students from the Department of Exercise Science at the University of Birmingham (mean ± s.d. age: 21.2 ± 1.1 years; body mass: 68.3 ± 5.2 kg; height: 1.77 ± 0.04 m). All experimental procedures were approved by the University Ethical Committee and were in accordance with the Declaration of Helsinki. Prior to their participation in the experiments, informed written consent was obtained from the subjects. Subjects underwent a practice session for the landings without vision (10 landings per drop height) 1 week before the experimental session to assess their capability to perform the task.

The barefooted subjects were instructed to start and terminate the landing movement in a standing position; to take off and touch down with both feet; to make a short step off the platform at take-off; and finally to brake the drop smoothly. The start of all drops was self-initiated. Subjects performed 10 drops from each height, had a 5 min rest to prevent fatigue before performing 10 drops from the next drop height. The order of the drop heights was randomised.

Mats were placed around the perimeter of the force platform. Each landing was monitored closely by two assistants, one standing on each side of the force platform.

**Experiment 1.** After blindfolding, the subjects were required to step onto the flat platform of a hoist, which was then raised gradually to the landings without vision (10 landings per drop height) and finally to brake the drop smoothly. The start of all drops was self-initiated. Subjects performed 10 drops from each height, had a 5 min rest to prevent fatigue before performing 10 drops from the next drop height. The order of the drop heights was randomised.

**Experiment 2.** A control experiment, performed 1 week after experiment 1, consisted of landings from the same drop heights used for experiment 1, but without the blindfold (i.e. with vision).

**Apparatus and technical procedures**

**Ground reaction force.** A multi-component force platform (Kistler 9281 A11, Kistler Winterthur, Switzerland; resonant frequency in situ: 800 Hz) was used for measuring $F_z$ after touchdown. Proprietary force platform software and hardware (BioWare, Kistler Instrument) were used to collect and analyse the ground reaction force signal. Ground reaction force was recorded at a sampling frequency of 1 kHz. A pressure pad switch (A31222 KS. Nelsa, Wigan, UK) was placed near the edge of the platform of the hoist to determine the instant of take-off.

**Kinematic analysis.** Before starting an experimental session, eight markers were placed over key body landmarks on the right leg of the subjects: on the toe, fifth metatarsal joint, heel, lateral malleolus (ankle joint centre), head of the fibula, lateral epicondyle of the femur (knee joint centre), great trochanter (hip joint centre) and the base of the rib cage. The landing movements were then videotaped at a sampling frequency of 50 Hz. The effective resolution of the measurements was 0.1–0.2% of the field of view (1.25 m; i.e. 1.25 mm). To remove noise the kinematic data were filtered using a low-pass Butterworth filter. The cut-off frequency was chosen from the frequency analysis of a stationary point (i.e. the toe marker after touchdown).

The Peak 5 Motion analysis system (Peak Performance Technologies, Englewood, CO, USA) was used to digitise the markers. From these data the joint angles during the landings were obtained. Joint angles were defined as follows. For the hip joint, the angle is defined as 180 deg when the trunk and the thigh are aligned; decreasing values indicate hip flexion, and vice versa for hip extension. For the knee joint, the angle is defined as 180 deg when the knee is fully extended; decreasing values indicate knee flexion, and vice versa for knee extension. For the ankle joint, the angle is defined as 90 deg when the foot is at right angles with the shank; decreasing values indicate dorsiflexion and vice versa for plantar flexion. For both experimental protocols, each subject performed 10 landings from each drop height, 6 of which were used for the kinematic analysis (i.e. 1st, 2nd, 5th, 6th, 9th and 10th landings). The sampling of these specific trials was considered sufficient for an initial assessment of kinematic adaptation. As subsequent analyses of these data revealed only minor differences between the two conditions at these critical time points of practice (i.e. the beginning, middle and end of the practice), kinematic analysis was limited to six trials.

**EMG activity.** The electrical activity (EMG) of the soleus (SO), tibialis anterior (TA), rectus femoris (RF) and biceps femoris (BF) muscles of the right leg was recorded using bipolar silver electrodes. The electrodes, which were developed from an original design by Johnson et al. (1977), were part of an encapsulated amplifier that was mounted directly onto the skin. The common-mode rejection ratios at 50 and 500 Hz were >100 and >80 dB, respectively, while the bandwidth was 10–1000 Hz. Each electrode had a diameter of 10 mm and was at a fixed distance (centre to centre) of 17 mm from the other. Movement artefacts were checked by tapping the electrodes, by creating passive movements of the limb and by shaking the wires. No relevant artefact was found using these procedures. Crosstalk between the EMG signals from different muscles was also checked by examining alternate contractions of the muscles before starting the experiment. No crosstalk was present. The noise-to-signal ratio of the EMG signals was <5%.

Since the EMG recordings were performed in two different experimental sessions, measurements of the electrode placement were taken so that they could be repositioned accurately for every experimental session. This procedure is considered to allow a more reliable comparison between EMG traces collected on different experimental sessions (Gans & Gornick, 1980). To allow a comparison between EMG traces recorded in two different experimental sessions (i.e. ‘vision’ and ‘no vision’ experiments; see Figs 8 and 9), the EMG associated with maximal isometric voluntary contraction (MIVC) was recorded from each subject on both sessions. The MIVC EMG was then used to normalise the EMG amplitude recorded during landing. Subjects were required to perform three maximal isometric plantar flexions, dorsiflexions, knee extensions and flexions while recording
from the SO, TA, BR and RF, respectively. The duration of the recording was 2 s, with rest periods of 5 min in between. The EMG was full-wave rectified and averaged off-line over the 2 s period and the three contractions.

Signal processing

The EMG and force platform signals were sampled simultaneously by an analog-to-digital converter (1401 Cambridge Electronic Design, Cambridge, UK). The force platform signal (i.e. the touchdown) was used to trigger the EMG recordings. The trigger was set so as to record the EMG signals 500 ms before and 500 ms after touchdown. Touchdown was given the value '0' on the time axis. The EMG was recorded at a sampling frequency of 2 kHz.

Kinetic variables. The force platform signal allowed the measurement of peak \( F_z \) and its timing. The force platform signal was also used to measure the centre of body mass (CM) displacement and the centre of pressure (see below).

Kinematic variables. The following variables were measured from the digitised data: joint angles (hip, knee and ankle), the amplitude of peak rotation of each joint, and the time at which peak joint rotations occurred. By combining the force platform and digitised data, measurements of the following parameters were made: whole body CM position, CM peak displacement and the times at which peak CM displacement occurred.

The displacement of the CM in the vertical direction was calculated by integrating twice the acceleration (a) of the CM (\( \alpha_{CM} \)). The acceleration of the CM can be determined from \( F_z: \) \( a_{CM} = [F_z - (m \cdot g)]/m \), where \( m \) is the mass of the subject and \( g \) is the acceleration due to gravity. The initial condition for these integrations was the location of the CM at the instant of landing, which was obtained from the digitised video data. CM peak displacement was measured as the displacement relative to the CM height at touchdown.

EMG variables. The EMG variables measured were: EMG onset latency, pre-landing EMG duration, and pre- and post-landing EMG amplitude. These variables were computed after full-wave rectification of the EMG traces. The time period between take-off and the onset of EMG activity before touchdown was defined as EMG onset latency. The time between EMG onset latency and foot contact was defined as pre-landing EMG duration. The EMG activity averaged 100 ms before and after foot contact was defined as pre- and post-landing EMG amplitude, respectively.

The method for calculating EMG onset latency has been described elsewhere (Santello & McDonagh, 1998). In short, the onset is defined as the time at which the largest change in the rate of growth of the integrated rectified EMG occurs. This algorithm was used to distinguish the later continuous build-up of EMG activity occurring shortly before foot contact from the early bursts of EMG occurring after take-off. We were interested in quantifying the former activity, since this represents a strategy by which the muscle-tendon complexes of the leg are adaptively prepared to absorb the impact at touchdown.

Statistical analysis

The mean of the EMG and kinetic values from 10 landings was calculated for each subject. Six values from each subject were used for the kinematic analysis. The data were analysed using two-way ANOVA with repeated measures to determine whether drop height \( (F_{z,0,3}) \), vision \( (F_{z,0,3}) \) or the interaction between these two factors \( (F_{z,0,3}) \) had a significant effect on the variables studied. The interaction between drop height and vision is stated in the text only when significant. Where statistically significant effects were found \( (P < 0.05) \) Tukey’s post hoc test was used to determine the significance in the differences between the values found when dropping from a height of 0.2 m and the remaining drop heights. Since landings were performed in blocks of trials for each height and vision condition, ANOVA with repeated measures was used to determine whether practice had an effect on \( F_z \), CM, and pre- and post-landing EMG amplitude.

RESULTS

Effect of practice when landing without vision

Landing without vision presents several challenges to the motor system. One of these is that the exact time of impact cannot be accurately inferred before performing the first drop from any given height. The amplitude of \( F_z \) is another important, if not the most important, variable that cannot be predicted on the first trial. However, proprioceptive and vestibular information acquired through the first (or the first few) trial(s) might be used by the subjects to control subsequent movements (this process can occur because the subjects know that the drop height is maintained constant within each block of trials). Therefore, one might expect the following scenario: the amplitude of \( F_z \) produced on the first trial might be very large, as subjects might use larger levels of muscle tension to brake joint rotations, the onset of which cannot be accurately predicted. In contrast, subsequent trials would be characterised by \( F_z \) values of smaller amplitude, as subjects are better able to predict flight duration and/or \( F_z \). Our data, however, confirmed this prediction only partially.

Figure 1 shows \( F_z \) from three subjects and both landing conditions measured over the 1st, 6th and 10th trials. In the ‘no vision’ condition, the above prediction was confirmed in subjects 3 and 4, as they experienced larger forces on the first trial than on subsequent trials. This trend, however, was not found in all subjects. The \( F_z \) experienced by subject 2 on the first trial was of similar amplitude to that found on subsequent trials. In fact, for this subject the trend that we expected for the ‘no vision’ condition was found for the ‘vision’ condition (i.e. a larger \( F_z \) amplitude on the first trial than on subsequent trials). In the ‘no vision’ condition, peak \( F_z \) on the first trial tended to be higher than on subsequent trials in five subjects. No clear trend could be detected in the remaining three subjects. The clearest difference between the two landing conditions was that within each block of 10 trials, peak \( F_z \) was characterised by a larger variability and amplitude when landing without vs. with vision (these data are presented in the next section).

The CM displacement was also examined to determine whether a trend existed across trials. We chose to examine CM displacement because this variable summarises the net effect of individual joint rotations. We hypothesised that earlier on in the practice, subjects might absorb the impact through smaller ranges of CM displacement, as this might assist in maintaining balance when vision is not available. As for \( F_z \), however, we did not find consistent evidence for such trends in peak CM displacement. These
qualitative observations were confirmed by a quantitative analysis (ANOVA) that showed no significant effect of practice on any of the kinematic, kinetic or EMG variables in either landing condition. As no practice effect was found, the following sections focus on the results averaged across trials.

**Kinetic analysis: \( F_z \)**

Figure 2 shows the force traces averaged from six landings per drop height (subject 8). The \( F_z \) values for landings without vision showed sharp peaks that occurred with a latency of \(~20\) ms from foot contact. In this subject, these peaks were not found when vision was available. However, these early peaks were not common across all subjects. When vision was available, \( F_z \) decreased after the peak and followed a similar time course across all drop heights until \(~1.5\) s after foot contact. There were then minor deviations until the attainment of a static body posture. In contrast, there were differences in time courses of \( F_z \) across drop heights when landing without vision. These features were typical of all subjects.

When vision was not available, peak \( F_z \) values occasionally reached levels up to \(~12\) times body mass. Such magnitudes of \( F_z \) were never reached when landing with vision, where the maximum peak amplitudes were of the order of \(~8\) times body mass.

Another major difference between the two landing conditions was that when vision was not available, peak \( F_z \) values averaged for each drop height had a larger within-subjects inter-trial variability than in the 'vision' condition. The difference between the two landing conditions was greater for higher heights (i.e. 0.6 and 0.8 m). Here, the mean standard deviation of the peak \( F_z \) value, averaged across subjects for each height, was larger without vision than with it (on average, \( \pm 1113 \) and \( \pm 734 \) N, respectively).

Figure 3A and B shows the values of peak \( F_z \), and time to peak \( F_z \), respectively. As drop height increased, the peak \( F_z \) increased significantly (\( P < 0.01 \)) for both conditions. Landings without vision were characterised by significantly larger peaks of \( F_z \) (\( P < 0.05 \)). Time to peak \( F_z \) decreased significantly with drop height (\( P < 0.01 \)), but it was not affected by the visual condition.

**Figure 1. Effect of practice on vertical ground reaction force**

The vertical ground reaction force (\( F_z \)) from three subjects when landing from a jump height of 0.8 m is shown for the 1st, 6th and 10th trials (dotted, dashed and continuous lines, respectively), with the ‘no vision’ condition shown on the left and the ‘vision’ condition on the right. The scale of the time axis is expanded over the first 400 ms after touchdown to show differences between trials.
Kinematic analysis

Ankle, knee and hip joint angles. The ankle, knee and hip joint angles were calculated by digitising video recordings of six landings per drop height. A tendency towards increasing joint rotation with increasing drop height was found regardless of the availability of vision (Fig. 4, subject 7). In all subjects, this tendency was particularly clear in the knee and hip joints. In the subject shown in Fig. 4, removing vision caused a smaller hip excursion when falling from the higher drop heights. However, this feature was not typical of all of the subjects.

Two variables were measured: (1) joint angle at touch-down and (2) peak amplitude of joint rotation (Fig. 5). With regard to joint angle at touchdown, the foot tended to be more dorsiflexed and the knee more flexed the higher the drop (this trend was significant only for the knee joint, \(P < 0.01\); Fig. 5). When vision was not available, all joints tended to be more flexed at foot contact than when landing with vision \((P < 0.01;\) compare left- and right-hand top panels, Fig. 5). However, the modulation of joint angle as a function of either drop height or vision was small. The knee joint had the largest range of joint

Figure 2. Time course of \(F_z\) from landing with and without vision

The averaged traces \((n = 6\) landings\) of \(F_z\) from one typical subject (subject 8) are shown. The top and bottom panels show traces from landing without and with vision, respectively. The numbers on each trace indicate the drop height in metres. The calibration bar shown in the lower panel \((1\) body weight, \(bw))\) applies to both panels.

Figure 3. Peak \(F_z\) and time to peak \(F_z\) vs. drop height

\(A\), peak values of \(F_z\) \((\blacksquare,\) no vision; \(\square,\) vision). \(B\), time to peak \(F_z\) values \((\blacktriangle,\) no vision; \(\triangle,\) vision). Both panels show values averaged across trials and subjects \((\pm S.E.M.)\). Asterisks indicate a significant difference \((P < 0.05,\) Tukey’s post hoc \(t\) test) between the value for that height and the value for 0.2 m.
rotation (17 and 9 deg, ‘vision’ and ‘no vision’ condition, respectively), whereas the range of joint rotation for the ankle and hip joints was 11 and 8 deg, respectively, (‘no-vision’), and 3 and 3 deg, respectively (‘vision’).

The bottom panel of Fig. 5 shows the values of peak joint rotation averaged across all subjects (± s.e.m.). The amplitude of peak joint rotation increased significantly ($P < 0.01$), as would be expected with increasing drop height for the knee and hip joints both with and without vision. This difference was significant only for knee joint rotation ($P < 0.05$). However, the absolute difference in peak knee joint rotation between the ‘vision’ and ‘no vision’ conditions was small (~8 deg).

Time to peak joint rotation tended to increase with increasing drop heights in all of the joints measured (ankle and hip joints: $P < 0.01$; knee joint: $P < 0.05$; Fig. 6). However, this trend was not found in all subjects. For example, a very small range of time to peak joint rotation was found for subjects 2, 4, 6 and 8 (~30 and ~40 ms for the ‘no vision’ and ‘vision’ condition, respectively). In contrast, the range of time to peak joint rotation was larger for the remaining subjects (~100 ms for both conditions).

Although time to peak joint rotation on average tended to increase with increasing drop height, regardless of the availability of vision, two main qualitative differences were found between the two landing conditions: (1) the sequence through which the different joints reached their maximum excursion, and (2) the time lag between times to peak rotation among joints. Without vision (Fig. 6, top panel), the knee joint reached peak joint excursion first, followed by the ankle and finally by the hip joint (the only exception to this sequence was seen in landings from a height of 0.2 m). With vision (Fig. 6, bottom panel), there was, apart from drops from 0.8 m, no clear sequence in the time at which peak joint rotation occurred. Furthermore, with the exception of landings performed from 0.8 m, peak joint rotation was reached at very similar latencies from touchdown in all the joints. The same sequence (although with different time lags among joints) was found for landings without vision only when landings were performed from a height of 0.8 m. Removal of vision had a significant effect only on time to peak rotation of the knee joint ($P < 0.05$). It was decreased.

**Whole-body CM displacement.** The CM position throughout the landing movement was computed from digitised video data and force platform data (Fig. 7A; see Methods). When vision was not available, the CM at touchdown tended (n.s.) to be higher (i.e. at a greater distance from the landing surface) than when landing with vision (CM value at time ‘0’, Fig. 7A) and when landing from greater drop heights. The time course of

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**Figure 4. Time course of ankle, knee and hip joint rotation from landing with and without vision**

The ankle, knee and hip joint angles from touchdown (‘0’ on the time axis) to standing position are shown. A representative trace from each drop height is shown for one subject (subject 7; the dotted line, dashed line, thin line and thick line indicate landings from 0.2, 0.4, 0.6 and 0.8 m, respectively). The ‘no vision’ condition is shown on the left, and the ‘vision’ condition on the right.
CM displacement, however, was similar regardless of availability of vision (left and right panels, Fig. 7A). It should be noted that CM peak displacement, measured relative to the CM position at touchdown, was also similar in the two landing conditions.

Increasing drop height caused CM peak displacement to increase in a linear fashion, regardless of the availability of vision (Fig. 7B). Drop height had a significant effect on CM peak displacement ($P < 0.01$), whereas removal of vision did not. The time to CM peak displacement was
longer without vision than with it. The major difference between the two landing conditions was the range of values over which this variable spanned, the range being twice as large when vision was not available (Fig. 7C). Furthermore, with the exception of landings from 0.2 m, landings with vision were characterised by a lower variability than landings without vision, as indicated by the standard error bars. Although briefer time to peak CM displacements tended to be associated with higher drop heights (i.e. 0.6 and 0.8 m), the height from which subjects dropped did not have a significant effect on time to peak CM displacement. Similarly, the time at which CM peak displacement occurred was not significantly affected by removing vision.

EMG analysis

EMG recordings from SO, TA, RF and BF when dropping from the 0.2 and 0.8 m drop heights are shown in Figs 8 and 9, respectively. The recordings shown in both figures are averages of five landings from the same subject (subject 3). Since landings with and without vision were performed at different experimental sessions, the calibration bars are expressed in units normalised to the EMG amplitude recorded during a maximal voluntary contraction.

It should be noted that the temporal patterns of muscle activity were similar, regardless of the availability of vision (compare left and right columns in Figs 8 and 9) and drop height. Specifically, muscle activity started at similar latencies from foot contact (i.e. ~100 ms; this is particularly clear when landing from higher heights – see Fig. 9). It should also be noted that the amplitude of muscle activity before touchdown was similar, regardless of the availability of vision. A similarity in the EMG temporal and amplitude characteristics was found across all subjects. With regard to the effect of drop height on EMG amplitude, we found different relationships between these two variables across subjects (see below).

The muscle activity observed after touchdown was found to occur mainly during the early part of the joint rotations. The major part of SO and TA EMG activity occurred during the first 150 ms after foot contact. This activity was characterised by several peaks occurring at a latency of 40–200 ms from touchdown. The main differences between traces from the two landing conditions were that the EMG activity tended to last for a longer period and to be of larger amplitude when vision was not available. Another finding was that RF and BF did not show a consistent pre-landing muscle activity before foot contact. In contrast, muscle activity in the RF muscle was always found throughout the whole period of knee flexion after touchdown.

EMG amplitude

EMG activity before touchdown. The EMG activity amplitude of SO, TA, RF and BF was averaged over a period of 100 ms before touchdown. We found a tendency for EMG pre-landing activity amplitude to increase with increasing drop height in all muscles and regardless of the availability of visual information, although to different extents across muscles and subjects. This tendency was quantified by linear regression analysis by computing the coefficients of determination ($r^2$) of the relationship between EMG amplitude before touchdown (averaged across 10 trials for each height) and drop height. The $r^2$ values, averaged across subjects, ranged from 0.51 ± 0.33 (BF) to 0.80 ± 0.24 (TA) when landing without vision.

Figure 7. Whole-body centre of mass displacement

A, the time courses of whole-body centre of mass (CM) displacement for one subject (subject 4; the dotted line, dashed line, thin line and thick line indicate one landing from a height of 0.2, 0.4, 0.6 and 0.8 m, respectively). The ‘no vision’ condition is presented on the left, and the ‘vision’ condition on the right. The ‘0’ on the ordinate indicates the CM position when standing. B, CM peak displacement values averaged across all subjects (± S.E.M.) from ‘no vision’ and ‘vision’ conditions (■ and □, respectively). Asterisks indicate a significant difference ($P < 0.05$, Tukey’s post hoc t test) between the value for that height and the value for 0.2 m. C, averaged time (in seconds) to CM peak displacement (± S.E.M.) from the two landing conditions plotted against each other. The numbers on each trace indicate the drop height in metres. A reference line with slope = 1 has been drawn to highlight the differences between the two conditions.
and from $0.53 \pm 0.40$ (BF) to $0.91 \pm 0.07$ (RF) when landing with vision. RF EMG amplitude tended to increase linearly in most subjects, regardless of the availability of vision, whereas the relationship between EMG amplitude and drop height was more variable across subjects in the remaining muscles. When landing without visual information, the pre-landing EMG amplitude tended to be larger than when landing with vision (Fig. 10A). This was particularly evident for the TA and RF. Removal of vision, however, did not have a significant effect on the amplitude of pre-landing EMG activity. A significant effect of drop height ($P < 0.05$) was found for the pre-landing EMG amplitude of the SO, TA and RF, but not for that of the BF.

**Figure 8. EMG activity during landing from a drop height of 0.2 m with and without vision**
The rectified EMG recordings from the tibialis anterior, soleus, rectus femoris and biceps femoris muscles (TA, SO, RF and BF, respectively) during landings from a 0.2 m drop height are shown for ‘no vision’ and ‘vision’ conditions (left and right column, respectively). The traces are averages of five landings (subject 3). Dashed and continuous lines indicate take-off and touchdown, respectively. Calibration bars, expressed as a percentage of the EMG amplitude recorded during maximal voluntary contraction, apply to both landing conditions.

**Figure 9. EMG activity during landing from a drop height of 0.8 m with and without vision**
Rectified EMG recordings from the TA, SO, RF and BF muscles during landings from a 0.8 m drop height are shown for ‘no vision’ and ‘vision’ conditions (left and right column, respectively). The traces are averages of five landings (subject 3). Dashed and continuous lines indicate take-off and touchdown, respectively. Calibration bars, expressed as a percentage of the EMG amplitude recorded during maximal voluntary contraction, apply to both landing conditions.
EMG activity after touchdown. The EMG activity amplitude of SO, TA, RF and BF was averaged over a period of 100 ms after touchdown. As found for the pre-landing EMG amplitude, removal of vision did not have a significant effect on the EMG amplitude after foot contact. However, in both landing conditions the EMG amplitude after touchdown tended to increase with increasing drop height in all muscles (Fig. 10B).

The $r^2$ values, averaged across subjects, ranged from $0.57 \pm 0.37$ (BF) to $0.89 \pm 0.09$ (RF) when landing without vision, and from $0.64 \pm 0.23$ (BF) to $0.89 \pm 0.09$ (RF) when landing with vision. As found for pre-landing EMG amplitude, in RF and SO the EMG amplitude tended to increase with drop height in both landing conditions, whereas the relationship between post-landing EMG amplitude and drop height in the remaining muscles was more variable. As for the amplitude of pre-landing EMG activity, the largest change in EMG amplitude was found in RF (Fig. 10B).

Drop height had a significant effect ($P < 0.05$) on the post-landing EMG amplitude of SO, TA, RF and BF. As found for the pre-landing EMG amplitude, removal of vision did not have a significant effect on the EMG amplitude after foot contact.

EMG timing. The time period between take-off and the onset of EMG activity during the fall, defined as EMG onset latency, tended to increase with increasing drop height, regardless of the availability of vision (Fig. 11).

When the drop height was increased from 0.2 to 0.8 m, onset latency increased by $+82 \pm 10\%$ and $+87 \pm 16\%$ for landings without and with vision, respectively (values averaged across muscles $\pm$ S.D.). The effect of drop height on the EMG onset latency from each muscle was significant ($P < 0.01$), whereas removal of vision was not.

Pre-landing EMG duration, defined as the time between EMG onset and foot contact, tended to increase significantly with increasing drop height (SO, TA, RF:

![Figure 10. Pre- and post-landing EMG amplitude vs. drop height](image)

EMG amplitude of activity in the SO, TA, RF and BF muscles, was averaged 100 ms before and after touchdown ($A$ and $B$, respectively). The EMG amplitude values, averaged across subjects ($\pm$ S.E.M.), are shown for each muscle (filled symbols show the ‘no vision’ condition; open symbols show the ‘vision’ condition). The values are expressed as a percentage of the average EMG amplitude recorded when falling from a height of 0.2 m. Asterisks indicate a significant difference ($P < 0.05$, Tukey’s post hoc t test) between the value for that height and the value for 0.2 m. Removal of vision did not have a significant effect on either pre-landing or post-landing EMG amplitude.
However, this tendency was clearer when landing without vision (top panel). When comparing the 0.2 and 0.8 m drop heights, pre-landing EMG duration increased on average by $+74 \pm 13\%$ in the absence of vision, whereas it increased only $+33 \pm 37\%$ when vision was available. In absolute terms, the largest range of values across SO, TA and BF was 25 ms. RF was the only muscle whose pre-landing EMG duration increased at a similar rate and range with increasing drop height (i.e. +78 and +85% in the ‘no vision’ and ‘vision’ condition, respectively). Therefore, in three out of four muscles the pre-landing EMG duration tended to remain relatively constant, regardless of drop height.

It should be noted that both the EMG onset latency and the pre-landing EMG duration increased at a similar rate with increasing drop height (i.e. similar slope) when vision was not available. However, the rates at which these two variables increased with increasing drop height were different when vision was available. Specifically, the rate of increase in EMG onset latency as a function of drop height was higher than the rate at which pre-landing EMG duration increased.

Removal of vision did not have a significant effect on pre-landing EMG duration. However, the interaction between drop height and vision was significant for the SO ($P < 0.05$), TA ($P < 0.01$) and BF ($P < 0.01$); the pre-landing EMG activity duration was longer when landing from increasing drop heights when vision was not available, as compared with landings with vision.

To assess the consistency in the control of pre-landing EMG duration, we compared the S.D.s of the EMG pre-landing durations, averaged across subjects, between landings with and without vision. One would expect larger S.D.s when vision was not available, as subjects might not be able to time EMG activity to foot contact as accurately as when vision was available. Contrary to our expectation, the range of S.D.s across all drop heights and muscles was very small ($< 20$ ms) and virtually identical between the two vision conditions (i.e. from approximately $\pm 16$ to $\pm 32$ ms).

**DISCUSSION**

We expected lack of vision to completely degrade the control of leg muscle activation. However, this did not happen. The most striking feature of our results is that overall, subjects performed landing movements in a similar manner, regardless of the availability of vision. Specifically, movements performed in the two conditions were adapted to different drop heights, as quantified by a similar peak CM displacements and similar joint rotations (with the exception of the knee; see below). With regard to the modulation of EMG activity, we found a similar scaling of EMG amplitude and onset latency to drop height in the two landing conditions (with subtle differences in the pre-landing EMG duration; see below). Nevertheless, there were some features of the movement that appeared to be different when vision was not available: (a) peak $F_z$, (b) peak $F_z$ inter-trial variability and (c) peak joint rotation sequence.

**Peak $F_z$.** First, landings without vision were characterised by larger values of $F_z$ than landings with vision (Fig. 3). This implies that lack of vision affected the control joint rotations after foot contact. Indeed, we found different temporal patterns of peak joint rotations when vision was removed; Fig. 6; see below). In contrast, Liebermann & Goodman (1991) reported that landing without vision resulted in similar, if not slightly smaller, peak $F_z$ values. However, an important difference between that study and ours is that their subjects were allowed to view the drop height before initiating the fall. This could explain the different results. Despite the different protocol and
the lack of kinematic and EMG analysis, the results reported by Lieberman & Goodman (1991) are useful for the interpretation of our results. Specifically, their findings suggest that vision can be used before initiating the fall to plan in advance the control of joint rotation after touchdown. More importantly, viewing the drop height before initiating the fall seems to compensate adequately for continuous vision when this is not allowed during the flight phase.

The larger peak $F_z$ values found in the ‘no vision’ condition are likely to be correlated with a greater resistance to joint rotations, and hence to a higher degree of muscle activation (i.e. muscle stiffness). The larger (although non-significant) amplitude of pre-landing EMG activity (in particular of the RF) found when landing without vision (Fig. 10A) might therefore be correlated with the setting of a higher muscle stiffness prior to landing. This interpretation is further supported by the fact that ‘no vision’ landings were characterised by smaller knee joint excursions (Fig. 5) and longer times to peak CM displacement (Fig. 7C).

$F_z$ inter-trial variability. A second important difference between the two landing conditions is that peak $F_z$ values tended to show a greater within-subject inter-trial variability in the ‘no vision’ condition than in the ‘vision’ condition. A greater variability was also found in the time to peak CM displacement. Taken together, these data suggest that when vision was not available, the movement was not controlled as consistently as when landing with vision.

Peak joint rotation sequence. The order in which the hip, knee and ankle joints reached their peak excursions was not affected by removing vision. Specifically, peak joint rotations occurred in a distal–proximal order (i.e. ankle first, followed by the knee and finally the hip joint). However, an important difference between the two conditions was that without vision the sequence of peak joint rotations was characterised by time lags that became more pronounced as drop height increased. In contrast, with the exception of landings from 0.8 m, peak joint rotations occurred at similar times when vision was available. Furthermore, knee joint rotation was smaller and faster when vision was not available than with vision. This finding suggests further that different patterns of leg muscle activation were used when vision could not assist the control of joint rotations and body segment orientation throughout the early phases of landing.

In summary, vision affected some, but not all, features of the movement. With regard to the features that were similar in the two landing conditions, it should be noted that these features are the kinematic variables measured at the end of the movement (i.e. peak CM displacement and joint rotation). In contrast, the features that were different were measured during the deceleration of joint rotations after foot contact (i.e. peak $F_z$ and time lags between peak joint rotations). Therefore, at a gross level, the overall skill did not seem to be greatly affected by removing vision. However, the differences that were observed suggest that different control strategies were used to compensate for the lack of continuous visual feedback.

Lacquaniti & Maioli (1989b) pointed out two alternative mechanisms for adaptation to the removal of visual information. At one extreme, the system required when deprived of vision might be able to substitute vestibular and proprioceptive sources of feedback to produce the same motor output. At the other extreme, the different sources of sensory input might produce a reorganisation of the motor output. In their study of adaptation to the suppression of visual information in ball catching, Lacquaniti & Maioli (1989b) found evidence for the second mechanism, since the adaptation was characterised by larger amplitudes in the post-impact EMG as well as larger and faster limb oscillations. The differences found in landing performance between the two experimental conditions in the present study would also favour a reorganisation of the motor output.

When vision is available, continuous feedback might be used to modulate preparatory muscle activity and/or kinematic variables such as joint angles or body segment orientation. In contrast, without vision subjects may have to use a trial-and-error strategy to learn how to build suitable patterns of muscle activity that would lead to a safe and smooth landing. Therefore, the first fall without vision might show a precautionary high activation of the muscles as the flight distance and duration, and the impact force cannot be predicted accurately. As subjects performed successive landings, they might have been able to learn the duration of the fall (which was constant within each block of trials) and the resultant $F_z$. If this were the case, one might expect values of $F_z$ to converge towards a smaller amplitude as subjects performed the movements from the 1st to the 10th trial. However, we did not find conclusive evidence for an effect of practice on either $F_z$ (Fig. 1) or any of the other variables measured. This suggests that subjects very quickly deployed a ‘default’ pattern of motor commands for each block of landings when visual information was not available. Specifically, it is likely that subjects adopted a strategy that could cope with a wide range of impact forces.

In our protocol, subjects landed from the same height within blocks of trials. However, other authors have addressed the question of non-visual adaptation to drop height using an alternative approach, by randomising drop height. Dietz and colleagues (Dietz & Noth, 1978; Dietz et al. 1981) reported that subjects adopted a default strategy when subjects fell forward onto a force platform (i.e. the onset of arm muscle activity preceding impact
occurred shortly after the onset of the fall). In contrast, muscle activity after touchdown seems to be of reflex origin, regardless of vision and drop height randomisation (Lewis et al. 1979). These data are consistent with a recent study performed by Duncan & McDonagh (2000) in which no short-latency EMG response was observed after subjects passed through a false landing platform. Our protocol was not designed to address the question of the origin of post-landing EMG activity. Nevertheless, our findings are consistent with those of Lewis et al. (1979), as we did not find significant differences in post-landing EMG amplitude between the two experimental conditions.

Control signals when landing with vision

As noted above, when subjects land from different heights, visual information, obtained both prior to take-off and online during the flight, can be used to adapt the control of the movement to different fall distances. In a previous study we quantified these adaptations as a scaling of pre- and post-landing EMG amplitude, and onset latency from take-off as a function of drop height (Santello & McDonagh, 1998). Our present results, now extended to upper leg muscles, are in general agreement with our previous findings. With the exception of the RF, pre- and post-landing EMG activity from all muscles tended to increase linearly with drop height (Fig. 10A and B, respectively). With regard to EMG timing, we have confirmed our previous results by showing that the onset of preparatory EMG activity after take-off increased with increasing drop height (Fig. 11). Although pre-landing EMG duration tended to increase with increasing drop height, a clearer modulation of EMG onset latency vs. pre-landing EMG duration indicates that muscle activity before impact was timed relative to the expected instant of foot contact, rather than to take-off (if this were not the case, EMG onset latency would be constant regardless of drop height). This strategy might ensure that the build-up of a desired level of muscle tension occurs throughout a relatively constant time window by increasing the rate at which EMG amplitude increases. These EMG timing and amplitude scaling mechanisms have also been found for catching tasks (Lacquaniti & Maioli, 1989a), and it has been suggested that they represent general strategies with which to control impact absorption tasks, regardless of the muscles and joints involved (Santello & McDonagh, 1998).

Control signals when landing without vision

Before discussing the possible mechanisms responsible for the results obtained in the ‘no vision’ condition, we should address a methodological issue about our protocol. We took every precaution to prevent the subjects from perceiving the height of the platform from which they initiated the drop. One of these precautions was to raise the take-off platform to its final position with the subject already standing on it. This was done before every trial to prevent the subjects from perceiving the drop height by stepping onto the platform just before take-off. It is possible that subjects might still have been able to infer the height of the platform by perceiving the time taken to raise it to its final position. However, this is unlikely as we repetitively raised and lowered the platform several times for each trial until the final height was reached. Therefore, we believe that subjects could not predict the drop height from which they were going to fall on their first landing. However, our protocol was designed to allow the subjects to infer drop height by integrating vestibular and proprioceptive information, made available by experiencing the height on the first (or first few) landing(s).

The ability to estimate accurately the time of foot contact in landing is obviously crucial since preparatory muscle activity has to be timed to the expected time of foot contact (Santello & McDonagh, 1998). Two main findings are of relevance. First, pre-landing EMG duration was characterised by similar inter-trial variability in both landing conditions. This suggests that when vision was not available, the integration of proprioceptive and vestibular information could compensate for the lack of visual information in timing pre-landing EMG in a consistent fashion. Second, when vision was not available, pre-landing EMG duration tended to increase as a function of drop height. In contrast, pre-landing EMG duration tended to remain relatively constant across drop heights when landing with vision (Fig. 11; Santello & McDonagh, 1998). This finding implies that the build-up of muscle tension was more accurately timed to foot contact when landing with vision than without it (i.e. when the exact time of touchdown could not be estimated accurately). This is because, in the absence of vision, the time at which foot contact will occur can only be inferred from the duration of the flight phase experienced in previous trials. In agreement with our results, Thompson & McKinley (1995) also reported a tendency for an increase in pre-landing EMG duration with increasing drop height when subjects landed without vision from randomised drop heights.

Larger peak \( F \) values might have been caused by the subjects’ inability to time the development of muscle tension at foot contact and throughout the subsequent joint rotations. Alternatively, starting the build-up of muscle tension earlier with respect to touchdown for larger drop heights might have been a precautionary measure to ensure the attainment of a sufficient level of muscle tension at touchdown. As mentioned above, the RF was atypical among all of the muscles studied, as it was the only muscle for which the pre-landing activity tended to increase with increasing drop height in a similar fashion regardless of the availability of vision. Furthermore, the RF was also characterised by the largest increases in pre- and post-landing EMG amplitude (Fig. 10A and B, respectively). If we assume that the attainment of a given level of tension at foot contact is
dependent upon the time at which pre-landing muscle activity starts, the difference in the EMG timing between RF and the other muscles could have been due to the need to build up larger forces in the RF as drop height increased.

Possible roles for visual information in the control of landing movements
Whereas evidence exists that vision is used during a flight to regulate body orientation (Bardy & Laurent, 1998) and pre-landing EMG activity (Vidal et al. 1979; Craik et al. 1982; Thompson & McKinley, 1995), it is still a matter of debate how visual information is processed to control the landing movement. When vision is available throughout the flight, it has been proposed that the time of contact could be extracted by the ratio between the displacement and the velocity of a moving image (i.e. the floor relative to the downward-moving body) on the retina (‘τ’, Lee, 1976, 1980; Lee & Thomson, 1982; Sidaway et al. 1989).

The onset of motor actions would be triggered when a critical value of τ (i.e. τ-margin) is reached during the movement. If a mechanism based on τ were used during landing movements, one would expect the onset of pre-landing EMG activity to occur earlier for falls from greater heights (i.e. the EMG onset after take-off would occur earlier). This is due to the fact that a given τ-margin would be reached earlier for falls when dropping from greater heights. However, our previous and present results on the onset of preparatory EMG activity indicate that the duration of pre-landing EMG activity tended to remain relatively constant. Furthermore, a τ-strategy would give unreliable estimates of time to contact for tasks characterised by relatively short durations, such as landing (Tresilian, 1995, 1999; Wann, 1996).

As pointed out above, viewing the drop height before take-off is sufficient to plan the control of joint rotations after touchdown such as to generate similar ground reaction forces as when vision is available during the fall. Therefore, it is likely that the visual estimation of drop height might be used to estimate flight duration and hence the resultant $F_c$. Through the repetitive practice of movements involving collisions such as landing, the motor system would map visual information about distance to the expected impact force by means of some form of sensorimotor memory. Such predictive mechanisms have been found to operate in motor tasks such as grasping (Johansson & Westling, 1987; Johansson, 1991) and catching (Lacquaniti & Maioili, 1989a; Lacquaniti, 1992). Obviously, this mechanism does not imply that continuous vision is not used during the fall. However, the very existence of such a mechanism (as also indicated by the findings of Liebermann & Goodman, 1991; discussed earlier), together with the ability of the CNS to compensate for the lack of continuous vision through the integration of alternative sensory modalities, point to the existence of several complementary mechanisms that might cooperate to assist in the control of landing movements.

Conclusions
Subjects were able to adapt the control of landing to different heights when visual information was withheld. This suggests that the system is capable of using non-visual sensory information to adapt the movement, as indicated by the kinematic similarities between the two landing conditions. Repetitive practice of the task would have provided the cues necessary to time and modulate EMG activity, the most likely cues being flight duration and $F_c$. However, proprioceptive and vestibular information could not fully compensate for the lack of visual information, as demonstrated by the larger and more variable $F_c$ values associated with landings without vision. Different temporal patterns of peak joint rotation also suggest that a reorganisation of the motor output occurred as a result of removing continuous visual feedback.

When vision is available during landing, the scaling of motor responses to different heights might depend upon the integration of visual cues acquired not only during the fall, but also those acquired before initiating the movement. It is likely that non-visual sources of sensory information are also used and are integrated with continuous vision, when this is available. Specifically, sensorimotor memories associated with previously experienced impact forces could be retrieved before initiating the movement by visually estimating drop height.


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