Preparedness for landing after a self-initiated fall

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CASTELLOTE JM, QUERALT A, VALLS-SOLÉ J. Preparedness for landing after a self-initiated fall. J Neurophysiol 108: 2501–2508, 2012. First published August 15, 2012; doi:10.1152/jn.01111.2011.—A startling auditory stimulus (SAS) causes a faster execution of voluntary actions when applied together with the imperative signal in reaction time tasks (the StartReact effect). However, speeding up reaction time may not be the best strategy in all tasks. After a self-initiated fall, the program for landing has to be time-locked to foot contact to avoid damage, and therefore advanced execution of the program would not be convenient. We examined the effects of SAS on the landing motor program in 8 healthy subjects that were requested to let themselves fall from platforms either 50 or 80 cm high at the perception of a program in 8 healthy subjects that were requested to let themselves damage, and therefore advanced execution of the program would not be convenient. We examined the effects of SAS on the landing motor program in 8 healthy subjects that were requested to let themselves fall from platforms either 50 or 80 cm high at the perception of a visual imperative signal and land on specific targets. In trials at random, SAS was applied either together with the imperative signal (SAS\textsubscript{vis}) or at an appropriate prelanding time (SAS\textsubscript{PL}). As expected, the latency of takeoff was significantly shortened in SAS\textsubscript{vis} trials. On the contrary, the timing of foot contact was not significantly different for SAS\textsubscript{PL} compared with control trials. No changes were observed in the size of the electromyograph bursts in the two experimental conditions with respect to the control condition. Our results indicate that the landing program after a self-initiated fall may in part be organized at the time of takeoff and involve precise information on timing of muscle activation. Once launched, the program is protected against interferences by external inputs.

...jump; motor program; startle

LANDING ON ONE’S FEET after a predictable fall requires activation of a motor program that should involve a precise and delicate equilibrium between flexor and extensor muscles to reach the appropriate degree of stiffness for a smooth contact with the floor (Dyhre-Poulsen et al. 1991; McKinley and Pedotti 1992; Santello and McDonagh 1998). The motor program for landing is of special interest in motor control studies. Apart from visual, somatosensory, and vestibular signals gathered at the time of takeoff and during the fall, there is no other recognizable sensory input triggering the execution of the motor program. Whereas takeoff can be to some extent delayed or advanced at will, landing after a fall must be time-locked to foot contact for safe landing. If the body position is maintained the same during the fall, the flying time is directly dependent on the height from where the subject falls. Usually, landing-related electromyograph (EMG) activity starts at about 100 ms before the time of expected foot contact with the floor (Santello and McDonagh 1998; Santello et al. 2001). Even though visual, somatosensory, and vestibular inputs may still be needed for feedback (Santello 2005), most features of the landing program should be determined by previous knowledge of height and contact surface characteristics (Jones and Watt 1971; Santello 2005; Santello and McDonagh 1998), which implies that landing movements rely more on preprogrammed than on feedback control. On the basis of this knowledge, we hypothesize that, once the landing motor program is set, it would not be convenient to receive any input that could interfere with the timing of foot contact.

It is known that, in a reaction time paradigm, highly prepared motor programs can be executed faster, without otherwise changing their configuration, when a startling auditory stimulus (SAS) is applied together with the imperative signal (IS), or at some time around it, in the context of the so-called StartReact effect (Carlsen et al. 2004; Queralt et al. 2008a, 2008b; Reynolds and Day 2007; Tresilian and Plooy 2006; Valls-Solé et al. 1999). The effect is likely due to the fact that fully prepared motor programs are represented in subcortical structures and circuits that can be accessed by the SAS, and therefore they can be triggered with no need for cortical processing of cue-related sensory signals (Carlsen et al. 2004; Valls-Solé et al. 1999). Alternatively, some authors have proposed that SAS speeds up the execution of a motor program by enhancing the perceptual processing or causing intersensory facilitation (Queralt et al. 2008b; Schmidt et al. 1984; Siegmund et al. 2001). As a major difference from the StartReact effect, intersensory facilitation would induce the effect by acting on the sensory domain, i.e., causing an increase in the total energy of the sensory input, whereas the StartReact effect would imply bypassing sensory processing because of the enhancement in the excitability of subcortical motor circuits responsible for task execution.

In this study, we aimed at assessing the effects of SAS on the landing program. We reasoned that although the StartReact effect would be present for the takeoff, there could be disturbing consequences for the timing of muscle activation if SAS were presented at the time of landing. We hypothesized that the motor program for landing might include some form of control of potential disruption by external sensory inputs and, therefore, that the StartReact effect would be blocked if it relies on subcortical motor preparation. However, an overload of sensory inputs could still have some effects if the program allows some feedback control of landing and intersensory facilitation is relevant for the StartReact effect. Apart from its physiological interest, we considered also the potential social and clinical benefit of increasing our knowledge about control of landing...
since falls are a frequent cause of work-related injuries (D’Souza et al. 2007; Mattila et al. 2008; Shishlov et al. 2011) and may become an important problem with advancing age (Peel 2011; Sturmiess et al. 2008). Therefore, we sought to know if the reaction to a SAS could have any role in braking the fine organization of the patterned motor program for landing.

METHODS

**Subjects.** Eight nontrained subjects (5 males and 3 females, mean age 35 yr, range 29—45 yr) volunteered to take part in the study. The subjects had no health problems and no physical impairment in the lower limbs at the time of testing. They were free from any neurological deficit that could affect the execution of the task. The study was approved by the Ethical Committee of the Hospital Clinic and a written consent form was obtained from each subject.

**Recording and stimulation.** Subjects were standing still over a large platform that could be placed at either 50 or 80 cm from the floor, facing a computer screen at a distance of 1.5 m. Subjects were asked to be ready to let themselves fall by placing their feet at the rim of the platform with the fingers out of support. They were asked to bend their knees at an angle of 10—20 degrees of flexion and to keep their arms hanging along the body. At floor level, at a distance of 15 cm before the platform, an area 50 cm wide and 50 cm long was marked as the landing area.

EMG signals were recorded at a sampling rate of 2,000 Hz from the right soleus (Sol), tibialis anterior (TA), rectus femoris (RF), and biceps femoris (BF) muscles with a pair of surface silver-silver chloride electrodes (0.7-cm diameter) attached to the skin overlying the bulk of the involved muscles. The startle reaction was monitored by recording the EMG activity from the orbicularis oculi with a pair of surface electrodes attached over the right lower eyelid. Three contact pad connections were used to record the takeoff and foot contact times: one was attached to the skin of the right foot just behind the head of the second metatarsal bone, another to the surface of the platform where the subjects stood for taking off, and the third on the surface of conductive material covering the landing area. The artifact generated by the separation between foot and platform connections marked the time of takeoff, and the end of the artifact caused by establishing contact between the foot and the landing area marked the time of foot contact. EMG signals from the four leg muscles and the orbicularis oculi were recorded with an electromyograph Mystro5Plus (Vickers Medical, Surrey, UK), set with a bandpass frequency filter at 50–1,000 Hz, a gain of 500 μV per division, and an analysis time window of 2 s. The EMG signals were fed, together with the signals from the pads and the imperative signal, into a personal computer equipped with an analysis program (Acknowledge, MP100; Biopac Systems, Bionic, Barcelona, Spain).

The imperative signal was a 5-cm² white square appearing over a black background on the computer screen situated in front of the subjects. A trial began when the experimenter warned the subject and pressed a computer key that, after a variable foreperiod (1–4 s), triggered the imperative signal and started the recording system. In test trials, SAS was produced by the discharge of a magnetic coil on top of a metallic platform (Valls-Solé et al. 1999). This produces a sound of an intensity of 130 dB (sound pressure level), measured with a Brüel and Kjaer type 2204 impulse precision sound-level meter, at a distance of ~2 m from the subject. The SAS was made to appear either together with the imperative signal or at a specific delay (see below). The screen sweep was used for a fast online perusal of the traces to exclude and repeat those trials that were unreadable because of artifacts.

**Procedure.** Subjects standing on the platform were requested to fix their gaze at the center of the computer screen to respond to the imperative signal by letting themselves fall gently, moving forward just enough to overcome the rim of the platform and land over the marked area. They were specifically asked to refrain from voluntarily flexing their knees further at onset of falling or moving the arms from the body sides to avoid adding height or unnecessary forward velocity to the maneuver. Subjects were allowed to practice a sufficient number of trials to be confident with the experimental setup. They were warned that some trials would contain a loud auditory stimulus (the SAS) that should be considered irrelevant for the task and were allowed to hear the SAS, but not during practice of the landing task. No additional instructions were given. Neither verbal nor visual motivation was provided during the trials. The interval between trials was 2 min, whereas a 30-min interval was given when the experimental condition was changed. Data collection began when subjects felt confident with the task.

The experiment was divided into two consecutive sessions, corresponding to the two conditions dependent on different timings of SAS delivery. In each session, there were two blocks according to platform height. For each block, we recorded 24 control trials and 6 test trials (containing SAS). SAS trials were intermingled pseudorandomly with control trials. We made sure that there was a minimum of two control trials between two SAS trials. In the first session, SAS was delivered simultaneously with the imperative signal (SASIS). In the second session, SAS was delivered before the estimated individual’s mean foot contact time, as a prelanding event (SASPL). The prelanding time was 250 ms for the 50-cm platform and 300 ms for the 80-cm platform. These different time windows were chosen to increase the probability of the SASPL to coincide with the appropriate timing before onset of landing-related EMG activity for the StartReact effect to occur (Santello and McDonagh 1998; Santello et al. 2001; Valls-Solé et al. 2008).

The effectiveness of the SAS in inducing a startle response was checked by monitoring the EMG activity of the orbicularis oculi muscle. SAS trials with no orbicularis oculi response were excluded, and additional test trials were included until recording a total of six trials containing EMG evidence for a reaction to SAS.

**Data analysis.** We assigned time 0 to the moment of IS presentation and divided the recordings in two phases: takeoff, from the IS to the actual separation of the foot and platform contacts, and landing, from the time of takeoff to the time the foot established contact with the floor. To avoid confusion with spurious activity during flight, the period of analysis for the landing phase was limited to the 300 ms preceding foot contact (Santello and McDonagh 1998). Task-related EMG bursts were identified as those showing a consistent rise in EMG activity larger than 2 SD above the averaged value of the individual’s 100-ms baseline preceding the IS. We considered an EMG event consistent when it was recognized in at least 20 of the 24 individual control trials by the 2 authors analyzing the graphs. Trials in which the onset of EMG activity could not be well identified (according to independent analyses by 2 of the authors) were not included. For each identified EMG burst, we measured onset latency and area. Onset latency of all events in the takeoff phase was measured from the IS, whereas that of the events in the landing phase was measured from both takeoff and foot contact times. We also measured movement-related parameters (time of takeoff and foot contact) and calculated the flight time as the time elapsed between takeoff and foot contact.

A two-way ANOVA was used to control between conditions. Sessions and heights. Data were further analyzed according to platform height (50 or 50 cm) and experimental condition (control, SASIS, and SASPL) by two-way repeated-measures ANOVA with condition and height as within-subject main factors. Mauchly’s test was used to test sphericity, and in case of nonfulfillment, degrees of freedom were corrected by using Greenhouse-Geisser estimates of sphericity (ε < 0.75) or the Huynh-Feldt correction (ε > 0.75). Post hoc pairwise comparisons were done with Bonferroni correction to compare levels when the main effect of condition was significant. For graphic representation, we chose to show data as means ± SD.
RESULTS

There were no incidences during the experiment, and the landing was safe and smooth in all trials for all subjects. There was a similar sequence of events in all subjects. In the EMG activity, we could recognize two separate groups of bursts: those related to the takeoff phase and those related to the landing phase (Fig. 1).

We first analyzed whether the events in the control condition were comparable in the two sessions. This was indeed the case in all parameters except for differences explained by the platform height (Table 1). For instance, latency of takeoff after IS was 979.1 ± 62 ms for the first session and 972.1 ± 65 ms for the second session at the 50-cm height, and it was respectively 967.6 ± 33 and 968.9 ± 36 ms at the 80-cm height. The first muscle activated in all conditions after IS was the TA, with a mean onset latency of 145.2 ± 24 ms for the 50-cm height and 160.3 ± 16 ms for the 80-cm height. Mean and SD values for the EMG activity in all muscles showed no differences between the two sessions (Table 1), including the EMG events related to landing, whether measured from takeoff or foot contact times.

As expected, flight time was longer for the 80-cm height than for the 50-cm height (F1,7 = 126.56, P < 0.0001), and there were height-related differences in the latency of the EMG activity when measured from the time of takeoff (Table 1).

Because no differences were found between sessions in any parameter, we pooled together data from both sessions in the control condition, separated for heights. A schematic summary of the timing of EMG events is represented in Fig. 2 for all conditions of the study.

Takeoff phase and flight time. The pattern of the events was similar in all experimental conditions (control, SASIS, and SASPL trials) and heights, as shown in Fig. 2. The first event observable at takeoff phase was silencing of the tonic low-amplitude background activity in the soleus that was accompanied at the same time or a few milliseconds later by a long-duration burst in the TA. Figure 3 shows the timing of all EMG bursts and takeoff, measured from IS. The two-factor ANOVA (platform height and conditions) showed a significant effect of condition on the latency of takeoff (F2,14 = 43.53, P < 0.0001) and onset latency of EMG activity for all muscles (F2,14 = 72.98, P < 0.0001 for TA; F2,14 = 89.69, P < 0.0001 for Sol; F2,14 = 78.27, P < 0.0001 for RF; F2,14 = 147.62, P < 0.0001 for BF) but no significant effect of platform height (F1,7 = 0.22, P = 0.7 for takeoff latency; F1,7 = 0.84, P = 0.4 for Sol; F1,7 = 2.31, P = 0.2 for RF; F1,7 = 0.49, P = 0.5 for BF) and no significant interaction (P > 0.05). Post hoc pairwise differences were seen for latency of takeoff as well as for all muscles between SASIS and either control

Fig. 1. Electromyograph (EMG) patterns in control and test trials from a 50-cm-height jump. Representative examples are recordings from 1 subject. A: control trial. B: test trial in which a startling auditory stimulus (SAS) was delivered at the same time (0 ms) as the imperative signal (SASIS). Note the marked shortening of reaction time for all events with maintenance of their temporal pattern. C: test trial in which SAS was delivered at 250 ms before the individual estimated landing time (SASPL). Flight time is shaded in gray along all traces. Note the EMG bursts grouped in 2 phases, before takeoff and foot contact times.
anterior muscles (see Figs. 1 and 2). They were followed by an tent bursts of simultaneous activity in the soleus and tibialis pertaining to the landing program was the presence of consistent with shorter flight time, onset latency of all landing-related EMG events measured from the time of takeoff appeared noticeably earlier (about 80 ms) for the 50-cm height than for the 80-cm height. 

Onset latency of all landing-related EMG events measured from 18 ms for the 50-cm height. Consistent with a shorter flight time, the differences in flight time (F1,7 = 859.45, \(P < 0.001\)) and, in this case, also a significant effect of platform heights, consequent with the differences in flight time (F1,7 = 260.57, \(P < 0.0001\) for TA; F1,7 = 623.38, \(P < 0.0001\) for Sol; F1,7 = 174.48, \(P < 0.0001\) for RF; F1,7 = 149, \(P < 0.0001\) for BF; F1,7 = 107.39, \(P < 0.0001\) for foot contact), without interaction among factors. Post hoc pairwise differences were seen for all muscles and for foot contact between SASIS and either control condition or SASPL (\(P < 0.001\) for all). No differences were seen between control and SASPL conditions.

The statistical analysis showed a significant effect of height on flight time (F1,7 = 859.45, \(P < 0.001\)), no significant effect of condition (F2,14 = 0.23, \(P > 0.8\)), and no interaction (F2,14 = 0.19, \(P > 0.8\)). The mean values after pooling all conditions together were 419.1 ± 21 ms for the 80-cm height and 337.2 ± 18 ms for the 50-cm height. Consistent with a shorter flight time, onset latency of all landing-related EMG events measured from the time of takeoff appeared noticeably earlier (about 80 ms) for the 50-cm height than for the 80-cm height.

**Landing.** The first EMG event identified within the epoch pertaining to the landing program was the presence of consistent bursts of simultaneous activity in the soleus and tibialis anterior muscles (see Figs. 1 and 2). They were followed by an irregular activation of muscles of the pattern that went on for some time after landing.

When events related to landing were measured from IS, a repeated-measures two-factor ANOVA showed again a significant effect of condition for EMG activity (F2,14 = 121.19, \(P < 0.0001\) for TA; F2,14 = 443.41, \(P < 0.0001\) for Sol; F2,14 = 81.16, \(P < 0.0001\) for RF; F2,14 = 53.87, \(P < 0.0001\) for BF) and foot contact (F2,14 = 42.71, \(P < 0.0001\)) and, in this case, also a significant effect of platform heights, consequent with the differences in flight time (F1,7 = 260.57, \(P < 0.0001\) for TA; F1,7 = 623.38, \(P < 0.0001\) for Sol; F1,7 = 174.48, \(P < 0.0001\) for RF; F1,7 = 149, \(P < 0.0001\) for BF; F1,7 = 107.39, \(P < 0.0001\) for foot contact), without interaction among factors. Post hoc pairwise differences were seen for all muscles and for foot contact between SASIS and either control condi-

| Table 1. Overall results of statistical analysis for takeoff and landing-related EMG events in control conditions |
|-----------------|-----------------|-----------------|
|                  | TO Events Measured From IS | L Events Measured From TO | L Events Measured From FC |
|                  | F       | P       | F       | P       | F       | P       |
| Soleus           |         |         |         |         |         |         |
| Height           | 0.01    | 0.943   | 30.34   | \(0.001\) | 2.27    | 0.175   |
| Session          | 0.00    | 0.987   | 0.06    | 0.818   | 0.02    | 0.899   |
| Height × session | 0.13    | 0.729   | 0.36    | 0.566   | 6.16    | 0.064   |
| Tibialis anterior|         |         |         |         |         |         |
| Height           | 1.62    | 0.244   | 37.02   | \(0.000\) | 0.00    | 0.966   |
| Session          | 0.06    | 0.818   | 0.02    | 0.913   | 0.09    | 0.412   |
| Height × session | 0.36    | 0.566   | 0.67    | 0.439   | 0.06    | 0.700   |
| Rectus femoris   |         |         |         |         |         |         |
| Height           | 0.15    | 0.707   | 20.65   | \(0.003\) | 0.74    | 0.419   |
| Session          | 0.03    | 0.873   | 0.02    | 0.873   | 0.07    | 0.718   |
| Height × session | 0.67    | 0.439   | 0.59    | 0.479   | 0.46    | 0.366   |
| Biceps femoris   |         |         |         |         |         |         |
| Height           | 0.01    | 0.923   | 55.78   | \(0.000\) | 0.07    | 0.800   |
| Session          | 0.03    | 0.866   | 0.02    | 0.821   | 0.07    | 0.725   |
| Height × session | 0.32    | 0.589   | 6.96    | 0.063   | 0.09    | 0.518   |

Values are F and P values for takeoff (TO) and landing-related (L) electromyographic (EMG) events in control conditions, determined using 2-way ANOVA. For all comparisons, degrees of freedom for between groups comparison is 1 and those for within group comparisons is 7. Statistically significant differences are marked in bold. FC, foot contact; IS, imperative signal.

Fig. 2. Mean values of EMG bursts recorded in control and test trials from a 50-cm-height jump. Schematic plot shows mean latency values of EMG recordings from all subjects for control, SASIS, and SASPL conditions. Each vertical bar represents the burst duration of each muscle. TO, takeoff; FC, foot contact; TA, tibialis anterior; Sol, soleus; RF, rectus femoris; BF, biceps femoris.

Fig. 3. Relationship between control and SAS conditions for takeoff. Values are means and SD of onset latencies from the imperative signal (IS) of TA, Sol, RF, BF and takeoff for each platform height (○, 80 cm; ■, 50 cm) and experimental condition (for each variable, bottom symbols correspond to control condition, middle symbols correspond to SASIS condition, and top symbols correspond to SASPL condition). *\(P < 0.05\) between SASIS and both control and SASPL conditions.
tion or \( \text{SAS}_{\text{PL}} \) \( (P < 0.001 \text{ for all}) \). No differences were seen between the control and \( \text{SAS}_{\text{PL}} \) conditions.

There were significant effects of platform heights in the latency of the EMG events related to landing when measured from foot contact \( (F_{1,7} = 20.6, P < 0.01 \text{ for TA}; F_{1,7} = 9.67, P < 0.05 \text{ for SOL}; F_{1,7} = 16.46, P < 0.01 \text{ for RF}; F_{1,7} = 19.73, P < 0.01 \text{ for BF}) \) but not for conditions \( (F_{2,14} = 1.91, P = 0.2 \text{ for TA}; F_{2,14} = 2.95, P = 0.1 \text{ for SOL}; F_{2,14} = 1.46, P = 0.2 \text{ for RF}; F_{2,14} = 1.15, P = 0.2 \text{ for BF}) \) without interactions. The mean latency after the values for all conditions were gathered together was 110.3 ± 9 ms for the SOL and 90.2 ± 15 ms for the TA for the 50-cm platform and 138.1 ± 7 ms for the SOL and 107.4 ± 12 ms for the TA for the 80-cm platform. Figure 4A shows all latency values for all variables related to landing, measured from foot contact, separated between 50- and 80-cm platform heights. Also, there were no significant effects of condition on latency of foot contact or related EMG events measured with respect to the time of takeoff \( (F_{2,14} = 2.52, P = 0.1 \text{ for TA}; F_{2,14} = 3.1, P = 0.06 \text{ for SOL}; F_{2,14} = 1.28, P = 0.3 \text{ for RF}; F_{2,14} = 2.9, P = 0.06 \text{ for BF}; \text{foot contact already reported above as flight time}). \) No changes in the pattern of EMG activity were seen among conditions, with consistently similar latency from takeoff for all conditions, separated for each platform height. There were significant effects of platform heights in the latency of the EMG events related to landing when measured from the time of takeoff \( (F_{1,7} = 145.44, P < 0.0001 \text{ for TA}; F_{1,7} = 96.11, P < 0.0001 \text{ for SOL}; F_{1,7} = 78.7, P < 0.0001 \text{ for RF}; F_{1,7} = 238.41, P < 0.0001 \text{ for BF}) \). Figure 4B shows all latency values for all variables related to landing, measured from the time of takeoff, separated between 50- and 80-cm platform heights.

**DISCUSSION**

The main result of our study is the absence of any effect of an appropriately timed SAS on landing after a self-initiated fall. The StartReact effect was indeed present at takeoff, in the same way as has been observed in other tasks \( (\text{Carlsen et al. 2004; Queralt et al. 2008a, 2010; Valls-Solé et al. 1999}) \), but when the SAS was given before landing, there was no noticeable response except for the burst in the orbicularis oculi muscle, characteristic of the auditory blink reflex \( (\text{Brown et al. 1991}) \). These observations are consistent with the idea that the motor program for landing is time-locked to foot contact and shielded to the potentially disturbing effects of a startle.

Various muscles participate in the execution of takeoff and landing programs. Takeoff results from the action of forward displacement up to the point of no return, beyond the edge of the platform surface \( (\text{McKinley and Pedotti 1992; Santello and McDonagh 1998; Santello et al. 2001}) \). We advised our subjects not to take upward impulse but to let themselves fall by a slight forward displacement, which is a difference with respect to other experiments on similar actions \( (\text{Feinland et al. 1999; Hara et al. 2005; Lees et al. 2004; Luhtanen and Komi 1978}) \). The fact that our subjects had an early activation of tibialis anterior with an initial soleus silence is compatible with a forward rather than an upward movement \( (\text{Crenna and Frigo 1991}) \). On top of that, the time taken for the subjects to travel the distance between the platform and the floor was fairly well adjusted to gravity laws \( (\text{the flight time was a mean of just 16.3 ms longer at the 50-cm height, and 13.2 ms longer at the 80-cm height, than what would correspond to a free fall for a rigid object not considering air resistance}) \), which speaks against the presence of additional time spent in an upward jump. Small variations among subjects and conditions in position at takeoff and landing strategy should account for the small differences with respect to the time that would be spent in a free fall.

The effect of SAS given together with the IS was to advance the latency of the whole pattern as a block, including the activity in muscles controlling the ankle joint and more proximal muscles. This is compatible with the entire program being accessible at a subcortical motor level, as described in previous studies \( (\text{Carlsen et al. 2004; Queralt et al. 2008a; Reynolds and Day 2007; Valls-Solé et al. 1999}) \), although a recent work by \text{Albiglou and McKinnon} (2012) has demonstrated that SAS triggers the program by faster accessing of the primary motor cortex. No significant differences were observed between control and test trials in flight time or in the intervals between onset of activation of different muscles, which is in accordance with the known fact that SAS does not modify the pattern of muscle activation except for the shortening of its execution.

Activity related to landing begins shortly before foot contact and consists mainly of activation of soleus immediately followed by tibialis anterior with the likely purpose of stabilizing the ankle joint in preparation for softening the impact. Before

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**Fig. 4. Relationship between control and SAS conditions for landing.** Values are means and SD of onset latencies measured in ms for the EMG events observed in the landing-related epoch for each platform height and experimental condition. Symbols are as defined in Fig. 3.A: values measured before foot contact. B: values measured from the time of takeoff. Time of foot contact for each condition is also included (top). Note that there were no significant differences between experimental conditions for all variables.
landing, no major joint rotations are observed and joint stiffness seems to be high (Liebermann and Hoffman 2005; Santello et al. 2001). Landing is not a reaction time to a specific IS, and its preparation does not seem to depend on will. It seems also independent from takeoff, because it occurs at a variable latency, according to height (Duncan and McDonagh 2000; Santello and McDonagh 1998). Instead, it is considered to be time-locked to landing (Duncan and McDonagh 2000; Greenwood and Hopkins 1976; Santello et al. 2001). One interesting observation is that leg muscles were activated slightly earlier in jumps from the 80-cm height than in those from the 50-cm height. We consider this logical if we take into account that, according to the laws of free fall, objects falling from higher levels reach a higher velocity at landing than those falling from lower levels and may require earlier and stronger muscle activation. This means that velocity when falling might contribute at least in part to triggering of the landing program.

The program for landing is distinct from all others that have been used so far for the study of the StartReact phenomenon. The special characteristics of the program for landing may be the reason why we did not find an effect of SAS on foot contact. The fact that SAS does not contribute to the timing of the landing program might be because the stimulus does not have access to the structures prepared for execution of the motor program. Also, our results indicate that there was no intersensory facilitation between SAS and the other sensory signals that are ongoing during the fall.

Absence of the StartReact effect. The landing program might be resistant to external modulation because it requires a timely, accurate, and smooth control of the end task. Co-contraction of antagonists has been seen from the beginning of the landing program, and muscular activity has also continued after landing, reflecting the need for preparatory muscular activity to stabilize joints to reduce impact (Liebermann and Goodman 2007). The reason for the absence of an effect of SAS is not the complexity of the program or the fact that the SAS is applied during an ongoing activity. In fact, the StartReact effect has been reported during execution of complex motor programs, such as obstacle avoidance (Queralt et al. 2008b), sit-to-stand (Queralt et al. 2008a), or gait initiation (Queralt et al. 2010), as well as during ongoing movement execution, such as with object interception (Tresilian and Plooy 2006) or stepping in unexpected directions (Reynolds and Day 2007). Possibly, the results of our study are more in line with those of Nieuwenhuijzen et al. (2000), who reported how the startle reaction was incorporated in the gait pattern of healthy subjects. Even if several peaks of activity were seen in different muscles and the step cycle subsequent to the startle was shortened, the results of their experiment showed that the responses were adapted to achieve extra stability, and there were only small changes in kinematics, allowing a smooth progression of gait. We think that the absence of an effect in the case of landing, a situation in which subjects have a learned knowledge of flight distance and time, is due to the fact that the motor program is not accessible to potentially disturbing inputs. The task is executed in the context of a critical disequilibrium. To avoid damage, the motor program might have been shielded to the interference of external stimuli.

The concept of shielding a motor program has some similarities with the findings reported by Carlsen et al. (2008) in another kind of time-restraint experiment. In that experiment, in which subjects had to perform a voluntary movement to release a key at a prespecified time, the authors hypothesized that the presentation of a startle did not interfere with the execution of the task due to the lack of advanced preparation. However, there are important differences between the two experiments. In the study by Carlsen et al. (2008), the action under study was part of a task and was dependent on the state of a joint as felt by subjects, described as time independent. Proprioceptive information was central to trigger the movement under study. In addition, in our paradigm, SAS has been applied at different times and heights before landing, with the same lack of effect.

Subjects may activate the landing program using an internal trigger based on experience. The dependence of motor coordination on time to contact was described as the “tau” model by Lee and colleagues (Lee 1976, 1980; Lee et al. 1999). Human landing has been explored according to this (tau) model to demonstrate that for heights <1 m, there is no evidence for a prelanding muscle timing based on a visual strategy (Liebermann and Goodman 1991). More recently, Liebermann and Hoffman (2005) studied EMG onsets of prelanding actions of highly experienced subjects, and their results suggested the use of a strategy that was insensitive to changes in visual flow. These authors argued that for this learned landing task, a feedforward mode of control may be implemented. Our results are in agreement with the tau model (Lee 1976, 1980; Lee et al. 1999), which is additionally supported by the absence of relevant changes in muscular activation times related to landing from different heights (Santello and McDonagh 1998; Santello et al. 2001).

Absence of intersensory facilitation. The landing program depends strongly on commands generated internally after previous knowledge, which implies the use of feedforward mechanisms (Craik et al. 1982; Santello and McDonagh 1998), the latter part being amenable to corrections by feedback information. In the case of self-initiated falls, feedback may be mainly due to vision, with some contribution of proprioception and vestibular systems. They may modulate small changes that appear during the ongoing of landing task, such as choosing different combinations of joint angles for different heights to get an adequate foot contact with the floor. In this context, intersensory facilitation could have occurred because of the auditory signal adding to the visual, proprioceptive, and vestibular inputs during the fall. However, absence of an effect of SAS indicates that the auditory stimulus did not significantly add to the sensory signals to modify the landing time.

Absence of intersensory facilitation may be due to various possibilities. First, visual transmission delays may hamper a useful processing of the continuous flow of information at the retinal level to anticipate events (Schlag et al. 2000). Second, the short duration of prelanding activity does not allow enough time for an adequate interaction to be expressed. Third, it may be a difficulty that the acoustic stimulus adds on a continuously changing visual input. Fourth, voluntary landing seems an already prepared program in which subjects, following the first trials, predict foot contact to absorb impact. Time to contact may be computed without a need for continuous vision, simply from an estimate of approach (Smeets et al. 1996; Tresilian 1991, 1993). A similar preparatory muscular activity has been seen in arm muscles when braking a fall (Dietz and Noth 1978; Dietz et al. 1981) or in catching tasks (Lacquaniti and Maioli...
In our paradigm, once the motor program for landing has been learned, it might be stored and fully prepared for execution time-locked with the expected landing. Visual inputs during falling are not strictly necessary to release the landing program at the adequate time (Liebermann and Goodman 1991; Santello et al. 2001). It has been consistently described that the role of proprioception in planning reaching movements seems to depend more on variations of target distances than on planning changes of direction toward the target (Sarlegna and Sainburg 2007; Sober and Sabes 2005). Because the voluntary fall is a programmed task and is performed in a constant distance, online use of proprioception may be secondary. Vestibular information may play a role in unexpected falls as an early muscular activity just following release, but it has not been described in voluntary falls or in those explored in subjects with labyrinthine defects (Greenwood and Hopkins 1976; Jones and Watt 1971).

Study limitations. Our study has a number of limitations. We recorded EMG activity in only four muscles and left unmonitored potentially important muscles such as paraspinal, arm, and neck muscles, and we did not use a movement transducer to record joint positions along the fall. Upper trunk and arm muscles might have been active during the fall and could have been differentially affected by the SAS (Brown et al. 1991). It is known that the sternocleidomastoid muscle is a key muscle for the recognition of the startle reaction (Brown et al. 1991). Therefore, since we did not record from it, we cannot be sure that a true startle reaction occurred in all trials in which the SAS was applied. Nevertheless, we recorded the auditory blink reflex from the orbicularis oculi, a response that behaves similar to the startle response in many respects. The orbicularis oculi response was present indeed when the SAS was applied before landing, even if there was no StartReact effect. In regard to the stimuli applied, we were interested in comparing SAS effects on takeoff and landing. However, we did not use stimulus intensities other than those potentially inducing a startle reaction. Lower intensity stimuli could have helped in further assessing possible intersensory facilitation effects.

In conclusion, we believe that during a self-initiated fall, subjects block external inputs irrelevant for the control of the imminent contact between feet and floor, and prime a top-down or goal-directed control over potentially disturbing sensory inputs such as the SAS, which might act as a distractor (Kawahara 2007). In our paradigm, we consider that the task, learned, is already sent feedforward in a top-down manner. The sensory systems may be coherent with the expected task and their joint contribution not accessed by SAS, with the result of absent StartReact effect and intersensory facilitation. Programmed landing requires performance of a timely fixed-patterned activity that should take into account impact absorption to prevent damage and reach a safe final position and that is protected from disturbing external interferences.

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DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS
J.M.C. conception and design of research; J.M.C., A.Q., and J.V.-S. performed experiments; J.M.C. and A.Q. analyzed data; J.M.C. and A.Q., and J.V.-S. interpreted results of experiments; J.M.C. and A.Q. prepared figures; J.M.C., A.Q., and J.V.-S. drafted manuscript; J.M.C., A.Q., and J.V.-S. edited and revised manuscript; J.M.C., A.Q., and J.V.-S. approved final version of manuscript.

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