

Movement control strategies during jumping in a lizard (*Anolis valencienni*)

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Abstract

Whereas maximal performance is subjected to specific control criteria, sub-maximal movements theoretically allow for an infinite number of control strategies. Yet sub-maximal movements are predominant in the locomotor repertoire of most organisms and often little understood. Previous data on sub-maximal vertical jumping in humans has suggested that a movement effectiveness criterion might best explain the observed control strategy employed. Here we test the generality of this criterion in jumping by inducing lizards to jump both at a range of distances as well as a range of take-off angles. Our results show that while movement effectiveness appears to best explain jumping for different take-off angles, a ‘push harder’ strategy (i.e. mostly increasing the force output of the system), is used in the control of distance jumping. Thus, our data support the generality of the movement effectiveness criterion for vertical jumping, but not for distance jumping. Sub-maximal distance jumping in the lizard *Anolis valencienni* appears to be governed by a relatively simple control strategy that allows a rapid response. This accords well to the ecological circumstances in which long jumps are typically used (escape from predators).

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1. Introduction

Jumping is a complex behavior involving the coordination of multiple segments to obtain the rapid displacement of center of mass away from its initial position (Bobbert and van Ingen Schenau, 1988; Aerts, 1998; Ashby and Heegaard, 2002; Gregersen and Carrier, 2004). Maximal jumping has been intensively studied and involves an optimization of the neuromuscular control (Bobbert and van Ingen Schenau, 1988; Selbie and Caldwell, 1996; Seyfarth et al., 1999; Spagele et al., 1999; Zajac, 2002; Hof, 2003). However, whether these same control strategies also apply to sub-maximal movements is unknown.

Yet, the majority of movements made by organisms are not maximal effort movements (Irschick and Losos, 1998), making it of paramount importance to understand how sub-maximal movements are controlled (Van Zandwijk et al., 2000; Vanrenterghem et al., 2004). As the control of sub-maximal movements can theoretically be achieved in an infinite number of ways underlying general principles are often invoked to simplify the control of complex movements (Van den Berg, 2000; Aerts et al., 2001). Two major control strategies for sub-maximal locomotor movements have recently been proposed in literature: (1) an increase or decrease of the force output of the system without changing the basic descending control and kinematics (Boyd and McLellan, 2002); (2) an optimization of the energy expended during the actual movement (Vanrenterghem et al., 2004). The biggest difference between the two

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strategies is that few changes in kinematics are expected in the first case. However, changes in kinematics involving the recruitment of light distal segments (foot, lower limb) before the heavier proximal segments such as upper limb or body (thus conserving energy when possible) are expected for the latter control strategy.

A recent study investigating the control of sub-maximal jumping in humans demonstrated that during vertical sub-maximal jumping, movement effectiveness is the most likely control criterion (Vanrenterghem et al., 2004). Movement effectiveness was associated with changes in the proximal segments and the invariance of changes in distal segment angles. Thus, energy expenditure was optimized during the jump by minimizing rotations of heavy proximal segments when possible (Vanrenterghem et al., 2004).

Here, the generality of the movement effectiveness criterion for jumping is tested by investigating the control of jumping in the lizard *Anolis valencienni*. *Anolis* lizards in general, are ideal subjects to study jumping as they often jump in their natural habitat to move around, or to escape from predators (Losos, 1999; Toro et al., 2003, 2004). As they live in complex three-dimensional arboreal habitats they not only jump different distances, but also jump to supports (branches) positioned at a wide variety of angles, distances and heights from the original perch. Movement effectiveness as a control criterion was tested for two different goal-directed jumping tasks in *A. valencienni*: jumping far and jumping at different angles, where jumping at different angles is used here as a proxy for vertical sub-maximal jumping. As an alternative control criterion the ‘push harder’ hypothesis is evaluated (i.e. increasing the force output of the system with few changes in kinematics; Boyd and McLellan, 2002). Specifically it is predicted that if movement effectiveness is the control strategy used, changes in distal segment angles (ankle, knee) during jumping should be constant and should thus have little or no predictive value for explaining changes in jump distance or take-off angle. Alternatively, changes in peak force should be strongly correlated with jump distance or take-off angle for the ‘push harder’ hypothesis to be valid.

2. Materials and methods

2.1. Animals and trials

Five individuals of the lizard *A. valencienni* (snout–vent length: 71 ± 4 mm) were used for the jumping trials. Before each trial, animals were placed in an incubator at 32 °C for at least 1 h. Animals were taken from the incubator, placed on the force platform and induced to jump to a branch set at different distances (range of jump distances: 4.6–37.7 cm) and heights (range of take-

off angles: 8.4°–55.4°). Each animal was induced to make at least five short, five intermediate, five long, and five steep jumps, thus providing a range of distances and take-off angles. Jumps were classified into categories based on the simultaneous video records (see below). Between jumping sessions (involving no more than three consecutive jumps) animals were allowed to rest for at least 1 h. All experiments were approved by the Tulane University IACUC.

Using a custom-made force plate (Heglund, 1981), the three-dimensional forces generated by the lizards while jumping were recorded (Toro et al., 2003, 2004). From the force records the total horizontal distance jumped, the peak total force and take-off angle were calculated for each jump (Toro et al., 2003). Take-off angle and jump distance were verified using video recordings (see below).

2.2. Kinematics

While jumping, lizards were videotaped in lateral and dorsal view (using a mirror placed at 45°; Fig. 1) at 250 Hz with a Redlake Motionscope PCI camera (Redlake, San Diego, CA, USA). The configuration of body and limbs was quantified at three discrete points in time throughout the jump using Peak Motus software: (1) at the onset of the jump, (2) at hands off, and (3) at take-off. The following markers (white paint dots) were digitized (see Fig. 1): 1: snout tip; 2: shoulder; 3: elbow; 4: wrist; 5: finger; 6: toe; 7: ankle; 8: knee; 9: hip; 10: center of mass; 11: tail tip; 12: first reference marker on the force platform; 13: second reference marker on the force platform; 14: third reference marker on the force platform; 15: right ankle in dorsal view; 16: hip in dorsal view; 17: left ankle in dorsal view. The center of mass was determined on specimens preserved with all legs flexed at 90° and should thus be regarded as an approximation of the actual instantaneous center of mass only.

From the coordinates of these markers the following angles were calculated: head tilt (defined as the angle between markers 1–2–9); elbow angle (2–3–4); wrist angle (3–4–5); trunk angle (2–10–9); knee angle (9–8–7); ankle angle (8–7–6); tail angle (10–9–11) and dorsal leg spread (15–16–17). As the center of mass was often hidden from view by the arm at the onset of jumping, the trunk angle was not calculated at that instant. Similarly, tail angle was not quantified at the onset of the jump as the tail tip was out of view during most trials.

Based on these kinematic variables we calculated the angular changes during the first (from onset to hands-off) and second (from hands-off to take-off) part of the jump separately, as well as the total angular change during jumping. These variables were then used in our multiple regression models (see below).

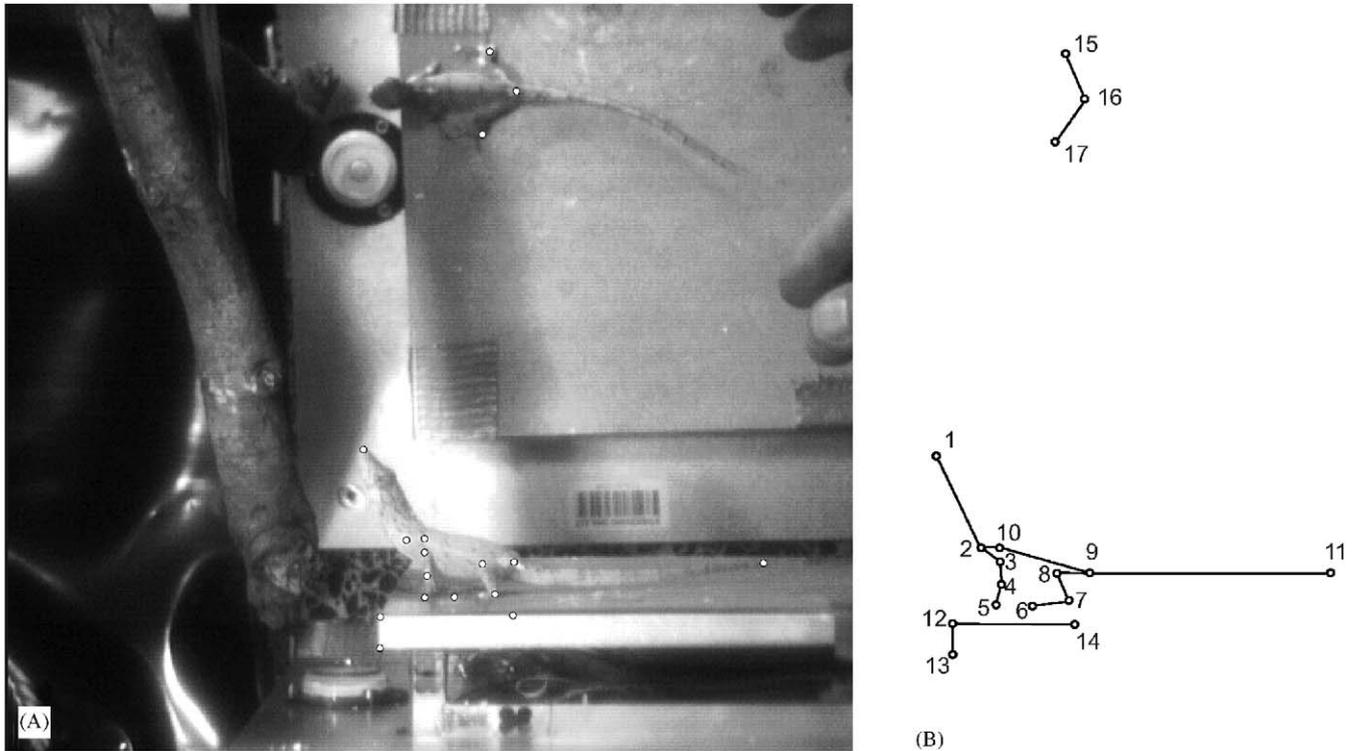


Fig. 1. Illustration of the experimental setup. (A) Lizards were placed on a force plate and induced to jump to a target (branch) set at different distances and/or heights away from the force platform. The camera was positioned laterally and a mirror, placed at 45° to the horizontal, provided a simultaneous dorsal view. White dots show reference points that were digitized to quantify the kinematics of jumping. (B) Graphical representation illustrating the different segments used for kinematic analysis (see Section 2).

2.3. Statistical analysis

All values were \log_{10} transformed before analysis. To investigate control strategies during jumping we used stepwise multiple regression analyses. First, control strategies employed for jumping farther (i.e. differences in horizontal jump distance) were tested by conducting a regression analysis with jump distance as the dependent variable and peak force during take-off as the independent variable. Second, a stepwise multiple regression analysis was run including both limb and body kinematics and peak force as independent variables. Third, to investigate control criteria used when jumping at specific angles, take-off angle (dependent) was regressed against peak force (independent). Finally, a stepwise multiple regression analysis with take-off angle as dependent and peak force and kinematics as independent variables was run.

3. Results

3.1. Kinematics of jumping in *A. valencienni*

During the preparation for jumping the hind feet are positioned in front of the pelvic girdle with both knee

and ankle angles extended beyond 90°. The front feet are placed at the level of the center of mass with the elbow flexed. During take-off, the knee and ankle angles initially decrease, after which they extend again to become maximally extended at take-off. Thus the animals appear to be using a counter-movement jump (Bels et al., 1992). The head and trunk are extended mostly during the second part of the jump. The forelimbs are extended until about halfway through the jump at which point the hands lose contact with the substrate. In general, the overall kinematics of jumping in *A. valencienni* accord well to those reported for other *Anolis* lizards (Bels et al., 1992).

3.2. Jumping for distance

Peak total force during take-off was highly significantly correlated with jump distance ($R^2 = 0.72$; $P < 0.001$; Fig. 2). Moreover, the slope of the regression of peak force to jump distance (0.96) was not significantly different from 1 ($t = 0.74$; $P > 0.05$) indicating that changes in jump distance are directly proportional to changes in peak force.

A stepwise multiple regression analysis with jump distance as the dependent variable and peak force and kinematics as the independent variables retained a

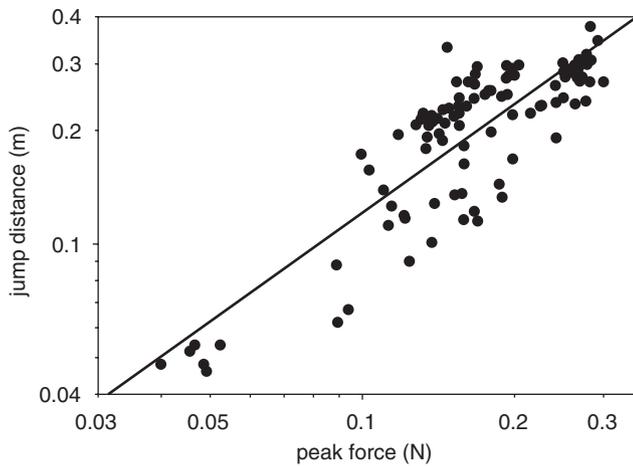


Fig. 2. Graph illustrating the near isometric correlation between the distance jumped and the peak force generated by the lizard during take-off ($R^2 = 0.72$; $P < 0.01$; slope = 0.96) suggesting that jump distance is linearly proportional to the force exerted during the push-off.

significant model ($P < 0.01$) including peak force, the change in knee angle during the second part of the jump, the change in head angle, the change in trunk angle and the change in ankle angle during the first part of the jump. This complex model improved the R^2 value to 0.86. An inspection of the standardized partial regression coefficients indicated that peak force ($\beta = 0.64$) and the change in head angle ($\beta = 0.21$) were the two most important kinematic variables contributing to the observed variation in jump distance.

3.3. Jumping for angle

Peak force during take-off was also significantly correlated to take-off angle, but explained only 14% of the variation in the latter ($R^2 = 0.14$; $P < 0.01$). The slope of the regression of peak force to take-off angle was 0.28 indicating that changes in peak force are clearly not linearly related to changes in take-off angle.

The stepwise multiple regression analysis retained a significant model ($R^2 = 0.60$; $P < 0.01$) with the change in trunk angle, the change in head angle and the change in elbow angle as the only variables (Fig. 3). This kinematic model explained 60% of the observed variation in take-off angle and did not include peak total force. An inspection of the standardized partial regression coefficients indicates that all three variables contribute approximately equally to the final model (trunk $\beta = 0.48$; head $\beta = 0.36$; elbow $\beta = 0.29$).

4. Discussion

Our results demonstrate that different control strategies are used in different modalities of jumping in *A.*

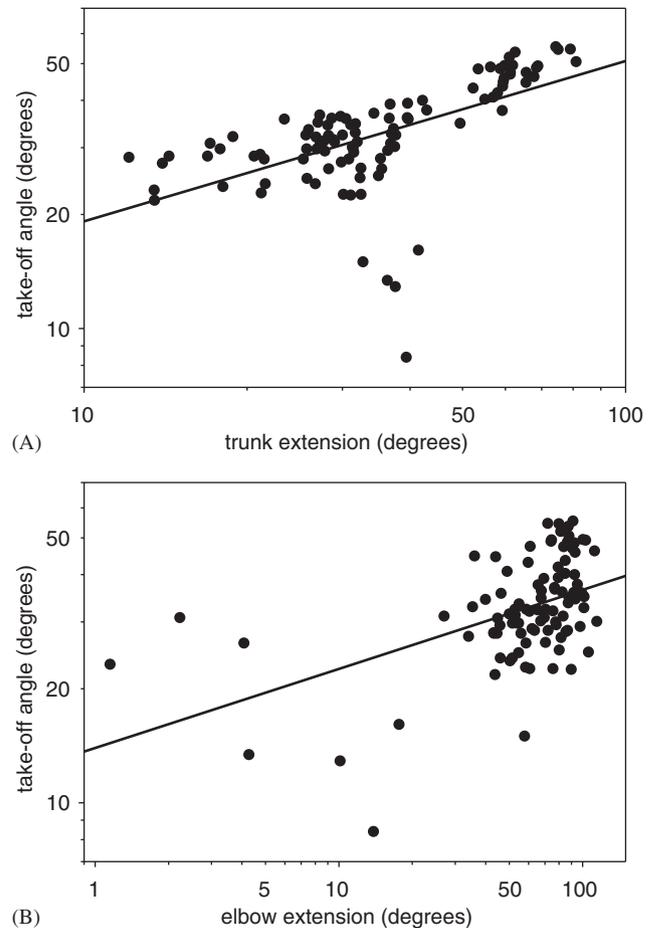


Fig. 3. Graphs illustrating the correlation between kinematic parameters including trunk extension (A) and elbow extension (B) and take-off angle. As the angular changes in the proximal-most segments were most significantly correlated with take-off angle (see Section 3) this strongly suggests a movement effectiveness control criterion when jumping at different take-off angles.

valencienni lizards. Distance jumping largely involved a simpler control strategy consisting of ‘push harder’ to jump farther. By incorporating only peak force during take-off into a regression model, 72% of the observed variation in jump distance could be explained. Moreover, changes in jump distance were linearly correlated with changes in peak force (Fig. 2). This monotonic response of distance to increasing force output appears to be an appropriate control strategy for the long jump, as has previously been suggested for swimming in larval lamprey (Boyd and McLellan, 2002). The strong correlation of peak total force to jump distance is not entirely surprising, however, as jump distance was calculated based on the force traces. However, it is still remarkable that peak total force was such a good predictor of jump distance across all trials given the variation in jump angle induced (i.e. from 8.4° to 55.4°).

The inclusion of additional kinematic variables improved the distance model to a total of 86% of the

variation explained. The angular changes included in the final model involved proximal segments such as head and trunk, but also distal segments such as knee and ankle. This is in discrepancy to the predictions of the movement effectiveness criterion, as in this case the recruitment of proximal segments should be more important than those of distal segments (Vanrenterghem et al., 2004).

Take-off angle was also significantly related to peak force, but the regression model explained only 14% of the total variation in take-off angle imposed. Moreover, upon the inclusion of kinematic variables in the model, peak force was no longer retained. Again, this is not entirely surprising as it is the proportion of vertical to horizontal force, rather than peak total force, that would be expected to be related to take-off angle. Yet, the kinematic model retained by the stepwise multiple regression accords well to the movement effectiveness criterion described for human vertical jumping. Although not as strong as the regression model for distance jumping, the kinematic model explained 60% of the variation in take-off angle. Important kinematic variables retained in the model were limited to changes in trunk angle, head angle and elbow angle, all being positively correlated to take-off angle. Although changes in elbow angle during the jump could be interpreted as postural changes aligning the body for the jump, other angular changes involved the proximal segments in the kinematic chain (head and trunk) as predicted by the movement effectiveness criterion. As these segments are also those with the greatest inertia, and as no changes in distal segments contributed to the model, these data support the movement effectiveness criterion (Vanrenterghem et al., 2004).

Although different control strategies appear to apply for different movement tasks, these strategies accord well to the situations in which these movements are performed. Jumping long distances is a behavior most often displayed by *Anolis* lizards as an escape response (Irschick and Losos, 1998) and the ability to execute the movement task quickly seems crucial. By mostly increasing the force output of the system (presumably by recruiting the muscles to a greater or lesser degree), the jump can be executed rapidly thus effectively carrying the animal away from the predator.

Jumping at different angles, on the other hand, is something that is often done in the complex three-dimensional habitat in which these animals live. During general locomotor tasks such as foraging and looking for mates, *A. valencienni* moves about much slower and typically jumps shorter distances from branch to branch and at different angles (Irschick and Losos, 1998). In these types of everyday locomotor activities, the animal can likely ‘afford’ a potentially more complex and time consuming control strategy. However, given the frequency and number of jumps executed, the movement

effectiveness criterion appears ideally suited as it may potentially save considerable amounts of energy on a daily basis.

Thus, our data show that different control strategies may apply for different movement tasks that are subjected to different ecological demands. Future studies of sub-maximal jumping in a wide variety of animals involving both distance and height jumping will be needed to confirm the generality of the data presented here.

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