

Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut?

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Abstract Tool use in apes has been considered a landmark in cognition. However, while most studies concentrate on mental operations, there are very few studies of apes' cognition as expressed in manual skills. This paper proposes theoretical and methodological considerations on movement analysis as a way of assessing primate cognition. We argue that a privileged way of appraising the characteristics of the cognitive abilities involved in tool use lies at the functional level. This implies that we focus on how the action proceeds, and more precisely, on how the functional characteristics of the task are generated. To support our view, we present the results of an experiment with five captive chimpanzees investigating the way how chimpanzees adapt to hammers of various weights while cracking nuts. The movement performed in the hammering task is analyzed in terms of energy production. Results show that chimpanzees mobilise passive as well as active forces to perform the compliant movement, that is, they modulate the dynamics of the arm/tool system. A comparison between chimpanzees suggests that experience contributes to this

skill. The results suggest that in tool use, movements are not key per se, but only in as much as they express underlying cognitive processes.

Keywords Goal oriented action · Tool use · Adaptation · Movement reconstruction · Mechanical energy · Cognition · Chimpanzee

Introduction

Since the classic Köhler experiment (Köhler 1925), where the chimpanzee Sultan was presented with a banana out of reach and two sticks, neither of which was long enough to reach the banana, tool use by apes has been the focus of many studies. However, in a recent paper, Byrne (2005) wrote a spirited plea for the study of apes' cognition as expressed in manual skills. The author called attention to the fact that the relationship between complex manual skills and cognition is generally ignored by researchers studying non-human primates. Indeed, tool use necessitates sequences of movements with objects in ways that plays significant challenges on the cognitive-motor system.

To raise Byrne's challenge, we propose in this paper an analysis of what is currently considered as the most complex technical skill mastered by non-human primates, that is, nut cracking (Boesch 1991; Inoue-Nakamura and Matsuzawa 1997; Sugiyama 1993). The study was carried out with captive chimpanzees. As the nut-cracking activity has been documented in several communities of wild chimpanzees, in Guinea (Biro et al. 2006; Sugiyama 1981; Sugiyama and Koman 1979), Ivory Coast (Beatty 1951; Boesch 1978; Boesch and Boesch 1981, 1982, 1984; Rahm 1971; Struhsaker and Hunkeler 1971), Liberia (Beatty 1951; Hannah and McGrew 1987) and Sierra Leone

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(Whitesides 1985)—we consider that an experimental study of nut cracking is an appropriate entry-point into manual skills as expressing apes' cognition.

Tool use has largely been studied from a cognitive perspective. The emphasis has mainly been on the conceptual foundation of tool use in cause-and-effect understanding of the functionally relevant properties of the physical and mechanical world. A few quite well-known situations, which have given rise to countless variations have been the focus of many questions on monkeys' and apes' "intelligence". A few among many others comprise the famous trap tube task (Visalberghi and Limongelli 1994; Visalberghi and Tomasello 1998), the hook retrieval situation that has given rise to a wide range of studies (Fujita et al. 2003; Hauser 1997; Povinelli 2000; Sugiyama and Koman 1979), the inverted rake problem or the rake and trap problem (Call and Tomasello 1994; Nagell et al. 1993; Povinelli 2000).

Almost all of these studies investigate the causal understanding and correlatively the mental representation underlying animal behaviour. From this perspective, scientists usually consider the ability to understand means-end relationships as a prerequisite and as the core of tool use by human and non-human primates. These experimental studies in captivity are based mainly, not on an analysis of the tool use activity per se, but on the choice of tools when the animal is presented with objects having various degrees of functionality to attain a piece of food. The experiments radically restrain the number of degrees of freedom of the task, many of them reducing the task to a choice between two options: in the hook situation, for example, used by Hauser (1997) and Povinelli (2000), the animal has the choice between two spatial arrangements. Similar settings characterise the inverted rake or the rake and trap problem. In these studies, cognitive capacity is inferred from how often a suitable tool is selected for solving the task at hand. More precisely, selection of an appropriate tool without engaging in a trial-and-error process is seen as an indicator of a mental representation of what a tool needed to solve the problem.

Yet these studies are more interested in the conceptual foundation of tool use and emphasise the underlying cognitive mechanisms rather than overt tool use performance. We consider here that this representational perspective does not address the full range of behaviour caught up in effective action in the real world. Understanding means-ends does not enable a person to extend his or her own capacity for action (Smitsman et al. 2005).

Following Byrne's claim, we argue that the cognitivist approach provides an incomplete picture of primates' cognitive capacities. Based on what is assumed to be the distinctive cognitive characteristics is known to be associated with tool use in *Homo sapiens*, Byrne (2005)

summarised the various features that should "offer guidance" for understanding apes' manual skills as follows (p. 32): precision handling, accurate aiming of powerful blows, bimanual role differentiation, regular and sequential plan, etc. Byrne also stressed the fact that the cognitive processes implied in tool use, as well as in any manual skill such as the manipulation of plant material, "deals with operations that change the physical world, often by *applying force...*". All these features are present in nut cracking. First, nut cracking requires a complex, i.e. high number of degrees of freedom, asymmetrical bimanual movement, which implies hand specialisation. Second, an optimal nut-cracking action necessitates adapting (1) the choice and use of tools to the nut, and (2) the movement to produce the right amount of functional energy (for a review see Foucart et al. 2005a).

In a very challenging and stimulating paper, Chiel and Beer (1997) discuss the need to "take into account the embeddedness of the brain in the body and world to understand cognition" (p. 556). In other words, intelligent behaviour is an emerging property of an agent embedded in an environment where he or she continuously interacts. This perspective has been embraced for a few decades by the ecological-psychology perception-action perspective that sees cognition as concretely embodied in performance. The perception-action approach, referred to as the ecological approach, sees cognition as being concretely embodied in performance and stresses the reciprocal role of the organism and the environment acting as a set of constraints from which behaviour emerges (Newell 1986, 1996; Reed 1988). The ecological view considers the interaction between the organism and the environment as the unit of analysis, rather than the organism by itself. The agent is participating in the world, but not controlling it. Action is considered as the result of the functional coupling between the organism and the environment. We endorse here the position of Reed (1988, 1996) who considered that the "action system approach" appears as more appropriate to the study of everyday life skills than a "passive observer" stance characteristic of an information-processing stance.

Following Newell (1986, 1996), we consider that three sources of constraints combine to provide the boundary conditions for carrying out an action: the organism, the task at hand, and the environment. The *organism* embraces the physiological, biomechanical, neurological, as well as cognitive and even affective facets of the agent. The *task* characteristics refer to its functional properties, i.e. what the organism (here the chimpanzee) has to do to successfully attain the goal. As far as nut cracking is considered, the task involves producing the right energy to crack open the shell. The *environment* comprises the universal constraints experienced by the organism (such as gravity or

temperature), and more local characteristics such as the tools (here, the hammer and anvil needed to crack the nut). Irrespective of the domain of behaviour under study, we consider that action must be defined as an emergent property of the interaction between these three sets of constraints. This means that action control cannot be understood if these different kinds of constraints are not part of the analysis.

The challenge: to find appropriate parameters to evaluate skill levels

When motor skills are the focus of interest, the cognitive view postulates that action depends upon, and is guided by, an internal pre-existing representation of different aspects of the movement. This “motor system approach” emphasises an information-processing perspective, the existence of some kind of “central representation”, “internal models” or “motor commands”. Along this theoretical position, the agent activity is directly caused by some kind of planning that controls the production of behavioural sequences. Consequently, most studies on motor activity in human and non-human primates concentrate on the kinematics of the movement as indexing motor control (see for non-human primates, Roy et al. 2000; Christel and Billard 2002).

Yet, the puzzling issue which is difficult to solve concerns the processes that bridge the gap between “representation” and behaviour, a “miracle”, to use Kunde’s (2001) words, often taken for granted. How an abstract action plan can be translated into a concrete motor behaviour? How is a single one chosen among the infinite number of equi-functional action/motor representations?

At variance with the previous perspective, we argue here that a privileged way of appraising the characteristics of the cognitive abilities involved in tool use lies at the functional level. This implies that we focus on how the functional characteristics of the task are fulfilled through the generation of a sequence of movements. It is not the movement per se which is the focus of the study, but rather how the functional action is rooted in the postures and movement considered as the necessary support of the action (Reed 1989; Biryukova and Bril 2008; Bril et al. 2000, 2005).

In addition, in the case of tool use, the tool appears as an implement that will modify the bodily resources (Smitsman 1997; Smitsman et al. 2005). Depending on its characteristics, the tool modifies the geometry, the dynamic and the information gathering process involved in the action. In the case of the use of a hammer in nut cracking, different hammers will modify the passive forces acting on the body each time in a different way. These changes can result in impediments that restrain action. Taking advantage of a

full-modified system, i.e. exploiting these changes as resources is a difficult assignment requiring years of practice.

Defining a percussion task

Before focusing on nut cracking, we need to understand clearly what percussion refers to. Percussion involves delivering a blow, or series of blows, in such a way that all the parameters and constraints of the task are fulfilled. This definition may be applied to many activities such as cracking nuts, hammering, drumming, hitting a tennis ball, etc. Mechanically speaking, success depends on the value of the impulse, which in turn depends on the momentum delivered at the time of contact. The momentum of the hammer is defined as the product of the mass of the hammer (m) and its velocity (v).

From a mechanical point of view, a blow is defined by the impulse produced, i.e. the momentum and duration of contact. For a biological system, the efficiency of a strike could be defined in terms of energy. In general terms, this energy is provided by the organism primarily through the transformation of chemical energy to mechanical energy through muscular activity. In terms of action and movement, energy is defined in two complementary ways: potential and kinetic energies defined as follows. Departing from the principle of conservation of energy, and if no additional—muscular—energy is added to the system, the sum of kinetic and potential energy stays constant. An object held in a person’s hand has potential energy—energy of position—which turns to kinetic energy—the energy of motion—when the person lets it drop to the ground.

The question is then how to evaluate the “strategy” used by the agent to produce the right amount of kinetic energy at the time of contact. If we consider that a biological system can use conservative mechanics¹, one extreme solution would be to rely only on the potential energy. This would mean that once the tool has been chosen, the agent has to control only the tool’s initial position, since the subsequent movement is passive (e.g. drop a stone).

However, a biological system can add a new kind of energy based on muscular activity. This means that in terms of movement, the agent can modify kinetic energy, and so the velocity. Hence, an infinite number of solutions can be used to produce the appropriate energy to meet the task constraints, depending on the two independent parameters that have to be selected: the initial position of the tool and the muscular force produced. We consider that

¹ Conservative mechanics: we consider here the ideal situation where there is no friction and no dissipation of energy, i.e. the total amount of potential energy is transferred in kinetic energy and reverse.

regulating the movement to achieve the composite end variable of energy delivered by the blow under variable conditions is a marker of cognitive activity.

Nut cracking: definition of the task

Nut cracking is defined as delivering a blow to a nut, in such a way that the shell cracks open leaving the kernel intact. To reach this goal, the agent (here a chimpanzee) must produce the right amount of kinetic energy (depending on the hardness of the shell) that will be transferred to the nut in order to produce an adequate deformation of the shell so that it breaks. Therefore, the kinetic energy of the hammer at the time of contact will be the main parameter to be controlled by the agent.

When making repeated strikes, to be efficient, the actor must discover how to produce kinetic energy on one hand, and avoid losing this energy during the impact, on the other. The blow must be elastic. In physics, an *elastic* blow is defined as a blow in which total energy is conserved (sum of potential and kinetic energies). This means that the total impulse is constant before and after the blow, that is, all forces are used to modify the velocity of the object, or to generate its deformation.

In nut-cracking, the result of an elastic blow may be the following:

- if not well anchored, the nut may shift away (no deformation, increased velocity of the nut)
- if well anchored on the anvil:
 - and if the force produced meets the nut's breaking point, the deformation breaks the shell leaving the kernel intact
 - and if the forces produced are greater than the breaking point, the shell is smashed and the kernel may be ruined

In the case of a *non-elastic* blow, a part or all of the forces are dissipated, and it will be difficult to crack open the nut. For example, if the nut is lying on a soft anvil, the energy will be absorbed by the support and the nut will not crack. Consequently, the way in which the action must be carried out depends on several factors, i.e. the weight of the hammer, the properties of the support surface and of the object to be hit, the velocity of the hammer, the orientation of the trajectory, etc.

Adaptations in nut cracking

The size and hardness of the nut and of the stone hammers, their shape and weight will never be the same. The

action—the striking movement—will have to be adjusted, being slightly different each time. This ability to perform an action, regardless of the situation, is the main feature of any skilled behaviour (Bernstein 1996).

This means that the choice of a “good” tool necessitates perceiving the relations between the nut's qualities, the tool's properties, and one's own “effectivities” (Bril and Foucart 2005; Gibson 1977, 1986; Matsuzawa 1994; Michaels 2003; Smitsman et al. 2005; Stoffregen 2000).

Observations in Bossou and in Tai clearly established the ability of chimpanzees to perceive the affordances of the nut-cracking task. In Tai, two types of nuts—*Coula edulis* and *Panda oleosa*—are regular items in the chimpanzee diet, with the shell of panda nuts being much harder than that of coula nuts. Boesch and Boesch (1981) reported that panda nuts are most often opened with a stone hammer, whereas both wood and stone hammers may be used for coula nuts. In addition, when only stones are used, Panda nuts require bigger, heavier and harder hammers than coula nuts. Another kind of adaptation is reported in Boesch and Boesch (1993). The choice of a hammer depends not only on the type of nut, but also on “where” the nut is being opened: coula nuts may be opened either on the ground or in trees. In the latter case, the hammer chosen is quite small; on the ground, bigger hammers are chosen.

This fine adaptation of the hammer to the hardness of the nut occurs in Bossou as well, even though there only palm nuts are available (*Elaeis guinensis*) (Biro et al. 2006). The ability to choose a tool that is finely adapted to the task may take a long time to develop. Fushimi et al. (1991) reported that in contrast to adult males who use a heavier tool and fewer hits to open the nut, adolescent and juvenile chimpanzees sometimes use hammers that are too light for the task.

The amplitude of the movement is considered to influence the force produced by the movement of the hammer. The amplitude of the movement used to crack open palm nuts with a stone hammer has been estimated as varying between 5 and 20 cm (Sugiyama and Koman 1979), while Fushimi et al. (1991) give an estimated range of 10–40 cm. Fushimi et al. (1991) emphasise the importance of fine-tuning the force to produce an efficient hit to open the shell without smashing the kernel. To our knowledge, only one study includes the quantitative estimations of such parameters of striking movements (Günther and Boesch 1993). Those authors and others have called attention to the precise control of forces required to open nuts without smashing them. Boesch and Boesch (1981, 1982, 1984) observed that when they open panda nuts (*Panda oleosa*) chimpanzees in Tai perform powerful hits at the beginning of the opening procedure, more gentle and precise ones afterwards. In order to estimate the strength of these two

kinds of hits, they noted the position of the hammer in relation to the chimpanzee's chest for a crude estimate of the amplitude of the movement. For example, a movement starting when the hand is positioned below the chest is considered typical of controlled and subtle hits. Unfortunately, those authors ignored the weight of the hammer, so there was no indication of the force produced during the strike. Fushimi et al. (1991) also described the necessary fine-tuning of force for producing an efficient hit. They observed one infant chimpanzee who typically failed to open palm nuts, suggesting that she was unable to adequately control force.

In the present study, we consider that the capacity to adapt, i.e. to generalise from each unique opportunity to act [what Thelen called the “here-and-now” dynamics (Thelen 1995, p. 95)], in novel but similar situations, gives access to cognition.

To assess this ability to adapt the everyday changing environmental world, we proposed an experimental setting that can be used for tool use studies with both human and non-human primates (Roux et al. 1995; Bril et al. 2005; Foucart et al. 2005a). The experimental rationale involves changing the properties of the tools while the goal remains the same, or in providing the same tools to attain different goals. In the present study, the chimpanzees had to crack open macadamia nuts with stone hammers of different weights. We hypothesise that chimpanzees adapt their movement in such a way to produce efficient strike characteristics.

Measuring physical parameters of action as a cue to understand adaptation

The experiment reported here concerns five captive chimpanzees who had to crack open nuts of different species using stone hammers of three different weights.

The challenge of behavioural studies on motor skills as a way to assess primate cognition lies in finding appropriate parameters and methods to evaluate the “efficiency” of the action depending on the conditions. We argued above that the action should be apprehended through physical measurements. In the case of nut cracking, we suggested that the best method for measuring the efficiency of a single strike is to measure energies before and during the blow. However, the strategy that leads to the efficient succession of blows has to be analysed as well.

In order to compute mechanical energy, the trajectories of the hammer are needed to be computed. This is why we first report the method we used for recording the movement of the upper arm that allows us to calculate the end-point displacement and velocity, as well as the potential and kinetic energy produced.

We consider that cracking a nut entails two types of control, a specific control to produce the right value of kinetic energy for one strike. Since for a given specie of nuts (that we consider here as homogeneous), the kinetic energy necessary to crack open the nut is constant, we hypothesise that a good control of the nut cracking action will be reflected in the adaptation of the production of kinetic energy, whatever the hammer properties be. That is, to produce a constant kinetic energy variation, the weight of the hammer should be compensated through variation in amplitude of the striking movement, that is, a variation in potential energy, and/or on the additional muscular force displayed.

In the other hand, the general control should be evidenced through the type of strategy displayed in the sequence of strokes to reach the right kinetic energy value. Observation of any primate cracking a nut shows that very seldom is the nut cracked open after only one stroke. Most of the time, a succession of blows is performed before the kernel can be extracted from the shell. If the animal were able to hit the nut only once to crack open the shell this would mean that he/she is able to produce very precisely the exact necessary kinetic energy at once. However, this is rarely the case and different strategies may be used to reach the goal. Two main categories of strategies are hypothesised. The first one includes the strategies where the animal reaches the goal through what we call a “blind” strategy, that is, by chance—the animal strikes random blows until the shell cracks. These strategies may lead to smashing the shell if the mechanical energy delivered is too high. In this case, we infer that the animal shows no memory of the sequence of strokes.

The second type of strategy could consist of producing low kinetic energy and increasing progressively up to the blow that will crack the shell. These strategies indicate that animals have some kind of “knowledge” of the relationship between amplitude of mechanical effect (strike efficiency) and amplitude of movement parameters (velocity, force, trajectory). However, two distinct cognitive levels should be distinguished. In the first level, only the need for an increase is taken into account. In a second level, both the increase and the final amplitude value of the mechanical parameter are taken into account. This second type of strategy hypothesises that the animal has the “knowledge” of the “value” of the breaking point of the shell and consequently the kinetic energy that must be delivered. In that case, the nut will never be smashed, as the efficient value of the kinetic energy will be approached through a sequence that takes into account at least the previous blows.

To test the existence of such strategies, we performed a statistical comparison between actual data and modelled data. In this first approach, we choose a couple of models that account for each strategy type.

Methods

Participants

Five chimpanzees (*Pan troglodytes verus*) from the Great Ape Research Institute (GARI, Okayama, Japan) named Loi (male, 9 years 5 months), Zamba (male, 9 years 5 months), Tsubaki (female, 8 years 10 months), Mizuki, (female, 8 years 1 month), Misaki (female, 6 years) participated in the experiment that took place in January 2005. The chimpanzees were cared for according to the “Guide for the Care and Use of Laboratory Animals” of Hayashibara Biochemical Laboratories, Inc., and the guidelines lay down by the Primate Society of Japan.

At time of the experiment, all of them were familiar with cracking nuts. Loi was the first to acquire the nut-cracking technique, during the period June–September 2002. During his training period, Loi learned to crack open macadamia and artificial nuts with stone hammers. In 2003, social learning sessions were performed three times a week with four other chimpanzees. Ten sites were provided, each with two anvils, ten stone hammers of different weights and 50 macadamia nuts. Loi was considered the model who should elicit nut-cracking behaviour in the other four chimpanzees. Zamba was the first to display nut-cracking behaviour by the 8th session, Tsubaki at the 11th session, Mizuki at the 13th session, and finally, Misaki at the 15th session. From September to December 2004, 35 additional sessions took place using the same protocol as the one used in the previous sessions. Thereafter, the four younger chimpanzees had additional sessions to improve their nut cracking skill: based on cracking artificial nuts with a 595 g stone hammer.

Procedure

The experiment was a “three tools by three types of nuts design”. The tools were stone hammers weighing 327, 595 and 1,039 g, designed in the text as 300, 600 and 1,000 g hammers. The hammers were of similar round shape. Their dimensions were $7.9 \times 7.5 \times 4.1$ cm for the 300 g hammer, $9.4 \times 8.3 \times 5.6$ cm for the 600 g hammer and $12.9 \times 12.2 \times 4.7$ cm for the 1,000 g hammer, respectively. The 600 g stone hammer was the one used in previous experiments. The three nut types were Brazil and macadamia natural nuts, and artificial nuts. Macadamia and artificial nuts were well known to chimpanzee, only Brazil nuts were new. The macadamia nuts weighed, on average, 6 g and were 25 mm in diameter. Their shell was about 2.7 mm thick. The artificial nuts were made of two plastic parts jointed by a metal belt. These nuts were 4 cm long and had a diameter of 3.3 cm. To make them as attractive as real nuts, they contained a fruit as a reward. The Brazil

nuts, triangular in cross-section, were approximately 4 cm long and their shell 3 mm thick. However, they were much easier to crack open than the macadamia nuts.

The three nut cracking sessions took place in January 2005. During one session, only one hammer was used. A session consisted in a chimpanzee cracking open eight artificial nuts, eight macadamia nuts and eight Brazil nuts. The granite stone anvil was the same for all session, a horizontal square anvil 37 cm of diameter and 7 cm high. The surface was characterised by a few cavities, two wide ones (approximately 5 cm of diameter and 1.5 cm deep) and 13 small ones, 1.8 cm wide and 1 cm deep (see Fig. 1).

Protocol

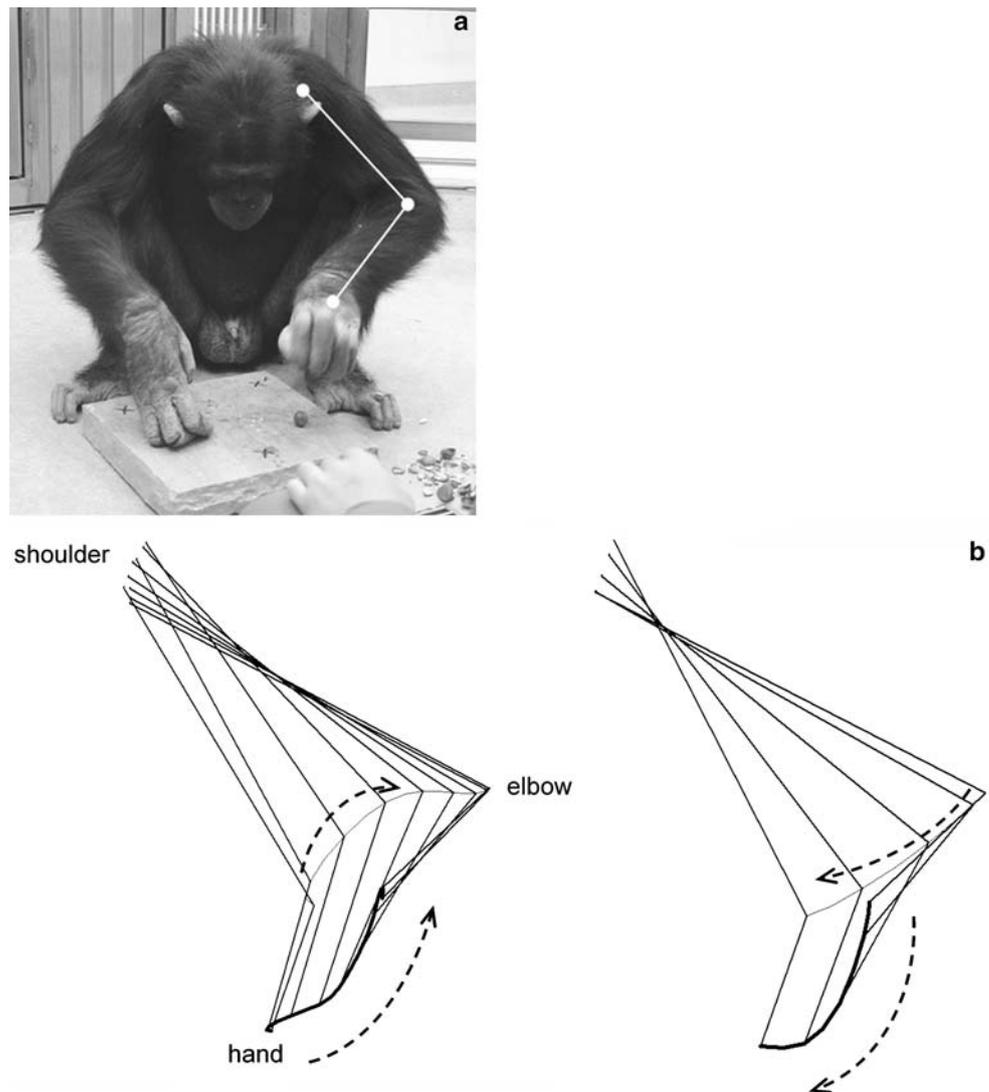
The chimpanzee was introduced in the experimental room by SH who first greeted him/her before starting the session. The nuts were presented one at a time, in rotation by species, starting with an artificial nut. The chimpanzees were allowed to eat the kernels. After having cracked a few nuts, the chimpanzee was rewarded with a piece of fruit or a little fruit juice. See S1 for an example of a chimpanzee, cracking a Macadamia and a Brazil nuts with a 300 g hammer. Only results on macadamia nuts are considered here². One session lasted for about 15 min. There were no two sessions within the same day. Two sessions were held usually one or two days apart.

Apparatus: recording modes and method of movement reconstruction

There are many ways of recording kinematics in the lab. Many of them use active (magnetic or ultrasonic devices) or passive markers (reflective or coloured markers). However, when animals or children are concerned, it can be difficult or even impossible to use any kind of marker. Hence, we need a more general method based on imaging measurement techniques (Winter 1979). Here, we used a multi-camera video-based system that allows the reconstruction of 3-D movement. As the chimpanzee was not constrained to stay in a fixed place, five video cameras recorded the chimpanzee during the whole nut cracking session (see Fig. 1). However, recordings from only two cameras (the best ones placed relative to the chimpanzee) were used for movement analysis.

² Artificial nuts could not be used in the analysis, as it is not possible to be sure of the strength of the closing. In addition the experimenter was giving “easy opening” artificial nut to a chimpanzee when he/she showed a decrease in interest as the artificial nut contained a fruit reward. This situation aroused the interest of the chimpanzees in the experiment.

Fig. 1 A chimpanzee participating in the experiment: **a** location of the *dots* selected for the 3D arm movement reconstruction during the nut-cracking task, **b** 3D stick diagrams of the upward and downward movements of the left arm (functional arm in that chimpanzee) during the fourth (and last) strike of a sequence of strikes performed with the light stone hammer (300 g) (one frame out of two)



Recording method

Five DV cameras were used to record the movement, to assure that the hand holding the hammer would be seen by at least two cameras (sampling rate 30 frames/s, or 60 de-interlaced frames/s). The recordings of two cameras only were digitised.

Camera calibration Camera calibration has two objectives: (1) intrinsic calibration involves assessing camera parameters, and (2) extrinsic calibration, or space calibration, is needed to reconstruct 3-D movement. For calibration, we used a general simple geometric model to calculate the transformation matrix between 2-D and 3-D worlds.

For intrinsic calibration, we used 2-D patterns (a black and white checkerboard) moving in front of each camera in order to calculate the focal length, the principal length and radial and tangential distortions. We used a calibration

technique based on the Zhang calibration approach (Zhang 1999).

In the second step, we used a similar technique to estimate extrinsic camera parameters for all cameras, i.e. their position and orientation. A fixed planar pattern must be seen by all cameras to determine the main reference frame. A triangulation technique was used to calculate the 3-D position of body reference points.

At the end of these two processes, we were able to define all the transformation matrices between the 2-D and 3-D coordinates. This means that we can relate the screen coordinates of one point visible to at least two cameras to its position in the real world.

This calibration phase is fully automatic and takes just a few seconds.

The calibration accuracy computed at the end of this process should be no less than 1/2,500 of the field of view. In our case, it is about 1 mm.

Camera recording The field of vision must be approximately the same for each camera. Camera sampling frequency must be chosen in accordance with the movement (rapid movements necessitate a high-velocity camera). For maximal accuracy, video cameras should be synchronised using a gen-lock. However, we digitally re-synchronised all the cameras in our calibration process (Yeaton and King 1999; Pourcelot et al. 2000).

Movement reconstruction

The reconstruction process was performed off-line and involved several steps³:

1. The video tapes were transformed into video files (de-interlaced frames).
2. Points were digitised manually.
3. 3-D reconstruction using the transformation matrices computed during the calibration phase.
4. Accuracy computation (mean error is around 1%). Precision depends on both the determination of the manual pointing precision and reconstruction error.

At the end of this process, the 3-D positions of the markers are computed. These markers are then used to calculate body segment positions and orientations. The full reconstruction of segments also necessitates a number of body segment parameters, which are mass, inertia, and centre of mass location. An anthropometric model is needed to compute these body segment parameters (BSP). These models may be either regressive using a database (Dempster 1939; Chandler et al. 1975) or geometric (Hanavan 1964).

3-D reconstruction of the striking arm movement Body segments were determined for each frame and for each camera, at shoulder, elbow and hand levels. Markers could not be used on the chimpanzee's body, except for the hand where the position was marked with a white spot between the proximal end of the first phalanges of the middle finger and of the third finger (see Fig. 1).

Following Günther and Boesch (1993), we used the Dempster model to calculate body segment parameters⁴. The main benefit of this model is that body weight is the only

³ Different software could be used for such calculation and analysis. For this experiment we used integrated software developed by the second author.

⁴ This model utilised for humans does minimise the weight of the chimpanzee's hand and this should be avoided in further studies. Here only juveniles took part in the study. We may consider that they do not have the adult anthropometric characteristics yet. The underestimation has relatively little or no consequence on parameters such as the ratio E_k/E_p . On the other hand, it does not change the significance of the comparison between hammer conditions.

parameter needed. The upper arm parameters computed from the chimpanzees body weights are given in Table 1.

Figure 1b shows the 3-D stick diagram of the front view of the (a) upward and (b) downward movement of the left arm during a strike using the light hammer. The stick diagram shows a significant movement of the elbow associated to the movement of the hammer. The shoulder shows a smaller displacement. The trajectory of the hammer is the result of the movements of the three upper arm segments: forearm, arm and hand-hammer (considered here as a single segment).

The movement of the hand along the three axes X , Y and Z , during an entire striking sequence using the light hammer is plotted in Fig. 2. The chimpanzee performed a sequence of seven strokes followed by a second sequence of five strokes.

Data analysis

We use the reconstructed 3-D trajectory of the hand-hammer during a strike to compute the values of the mechanical energy while the sequence of movements is performed.

Parameter computation: mechanical energy

As mechanical energy is considered the sum of potential and kinetic energies, the position and velocity of the hammer must be computed during the entire course of the movement (see Fig. 4).

The trajectory of the hammer is defined as the path of the hammer in 3-D space. The path provides two kinds of information: (1) a qualitative parameter, i.e. the shape of the path, and (2) quantitative parameters such as length and amplitude.

The instantaneous velocity of the hammer is defined as the derivative position of the tool. The simplest way to evaluate velocity (v) between two positions (p_1 and p_2) is given by the displacement per time unit: [$v = (p_2 - p_1)/(t_2 - t_1)$, t_2 minus t_1 is the time elapsed between the two positions p_1 and p_2] (Winter 1979).

Potential energy is the part of mechanical energy which is dependent on gravity (mg , mass times gravitational acceleration) and the gradient of vertical position (h) during the movement ($E_p = mgh$). When h equals zero, potential energy also equals zero. This base value depends only on vertical position and must be chosen according to the task. For percussive tasks, the vertical reference position is assumed to be the contact point between stone and nut.

Kinetic energy is defined as the product of the inertial mass and the square velocity, both in rotation and translation ($E_k = \frac{1}{2}mv^2$). The hand and hammer are considered

Table 1 Average body weight of the five chimpanzees at time of the experimentation in January 2005

Chimpanzee	Body weight (kg) in January 2005		Hand + hammer weight (kg)		
	Mean body weight	Hand weight	Light hammer 327 g	Medium hammer 595 g	Heavy hammer 1,039 g
Loi	60.640	0.364	0.691	0.959	1.403
Zamba	42.880	0.257	0.584	0.852	1.296
Tsubaki	44.480	0.267	0.594	0.862	1.306
Mizuki	30.980	0.186	0.513	0.781	1.225
Misaki	23.960	0.144	0.471	0.739	1.183

The hand weight is considered as being 0.6% of body weight

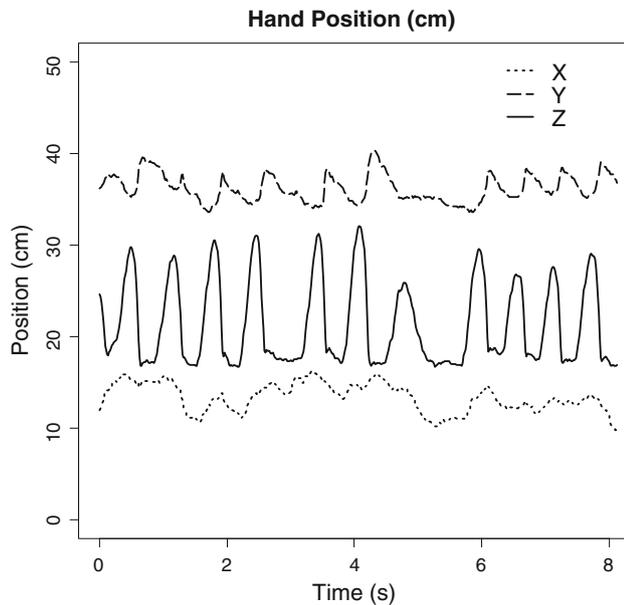


Fig. 2 Hand displacement along the three axis, vertical (Z), antero-posterior (Y) and medio-lateral (X) during a sequence of strikes with the light stone tool (0.327 kg) used to crack open a macadamia nut on the stone anvil. The origin corresponds to the right ground corner of the reconstruction space (reference frame that depends on calibration)

here to be one virtual point. Therefore, only the linear translation energy can be evaluated.

Ratio kinetic energy/potential energy In order to compare the energy flow between potential and kinetic energy, we calculated the ratio (r) of these two energies as: $r = E_k/E_p$. Kinetic energy is determined at the time of contact, and potential energy at the higher position of the hammer. For a conservative pendulum, the ratio is always equal to one. If it does not equal one, the ratio indicates the additional energy resulting from muscular force during the movement. This additional muscular force could act to accelerate ($r > 1$) or decelerate the arm movement ($r < 1$).

Stroke sequences analysis

For each nut cracked, sequences of strokes have been delineated from the entire course of the hammer kinetic

energy. A pause larger than one and half the stroke frequency was considered as the signal of a new sequence (see Fig. 4). After determining the number of sequences for each nut cracked, the inter strokes variation of amplitude, potential and kinetic energy was analysed and compared to five different models, each of them mirroring a striking strategy depending on the order parameter of the model. Two main types of strategies were defined: *blind strategy* models and *a priori knowledge* models. Both types of models are developed below.

Blind strategy models The first type was represented by a “blind strategy”. In this case, each stroke in a sequence could be considered as a constant value added with a white noise defined by the standard deviation (Eq. 1).

$$S_n = M + \zeta \quad \text{Model 1} \quad (1)$$

where S_n represents the stroke, M the mean value and ζ the noise.

However, actual data exhibited variations that could not be compared to random noise only. These fluctuations could be analysed with a more sophisticated model represented by a simple autoregressive model (Eq. 2).

$$S_{n+1} = \sum_{i=0}^{p-1} A_i S_{n-i} + \zeta \quad \text{Model 2} \quad (2)$$

where S_{n+1} represents the next stroke, A_i is the matrices of coefficients, S_{n-i} the stroke ($n - i$), p the order of the model and ζ the noise. We used a second order autoregressive model AR (2). In this case, each stroke value depends only on a weighted sum of the two previous values of the same series plus noise.

In these two models, the critical fracture value is reached using a random strategy depending on noise and/or previous stroke values.

A priori knowledge models The second strategy hypothesis was that the stroke value is defined by “knowledge” of the fracture critical value for a “standardised” nut (Fig. 3). This knowledge defines the initial condition of the model. The stroke has to be modulated to reach the actual fracture threshold (depending on each nut). Those models could be qualified as “a priori knowledge

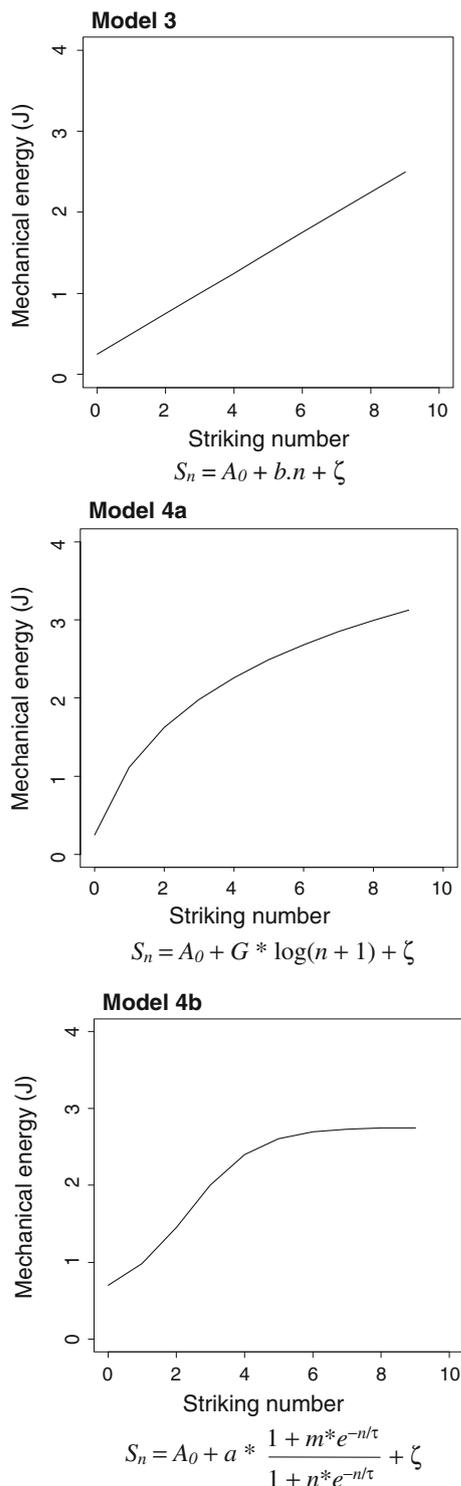


Fig. 3 Theoretical models of striking strategies over a sequence of strikes that constitute the “*a priori* knowledge” models (models 3, 4a and 4b)

models”. The simplest modulating model is represented by a linear increment (Eq. 3).

$$S_n = A_0 + b \cdot n + \zeta \quad \text{Model 3} \quad (3)$$

where S_n represents the stroke, A_0 the initial value, b the stroke increment value and ζ the noise. In this first linear model, only a low threshold (A_0) is needed and this simple strategy could lead to smashing the nut in the course of cracking it.

A higher threshold is required in the next two models.

$$S_n = A_0 + G \log(n + 1) + \zeta \quad \text{Model 4a} \quad (4a)$$

$$S_n = A_0 + a \frac{1 + m e^{-n/\tau}}{1 + n e^{-n/\tau}} + \zeta \quad \text{Model 4b} \quad (4b)$$

The first model (Eq. 4a) depends on the initial value (A_0) and a gain factor (G). However, the high threshold could be reached due to the logarithm function used as an increasing factor. To overcome this problem, we use a logistic function (Eq. 4b) that models an S-curve growth function. This model depends on four parameters defining the shape of the S-curve.

Statistical analysis

Statistics on individual strokes Factorial ANOVA was used to test the effect of the type of hammer on each of the parameters under study. In addition, we performed a post hoc test (Newman–Keuls) to compare the effect of the hammers’ weights two by two ($P < 0.05$).

Statistics on sequences of strikes In order to compare the models to actual data, simulated data were first calculated using the five different models for every sequence of strikes. In a second step, the two series of data [simulated and actual data of a sequence of strikes, i.e. kinetic (E_k) and potential (E_p) energies] were compared using a Pearson’s correlation coefficient, followed by a t test. The t test is used to establish if the correlation coefficient is significantly different from zero, and, hence that there is evidence of an association between the two variables for each sequence of strikes (actual data and simulated peak values of energies). The t value is calculated as followed:

$$t = r \times \sqrt{(N - 2)} / \sqrt{(1 - r^2)}$$

where r is the correlation coefficient and N is the number of strikes (Valleron 2005). We used $\alpha = 0.05$ to determine statistical significance.

Results

Analysis of individual strokes

Number of strokes necessary to crack open a nut

The 3D reconstruction of the end-point displacement was done for five macadamia nuts for each condition and for

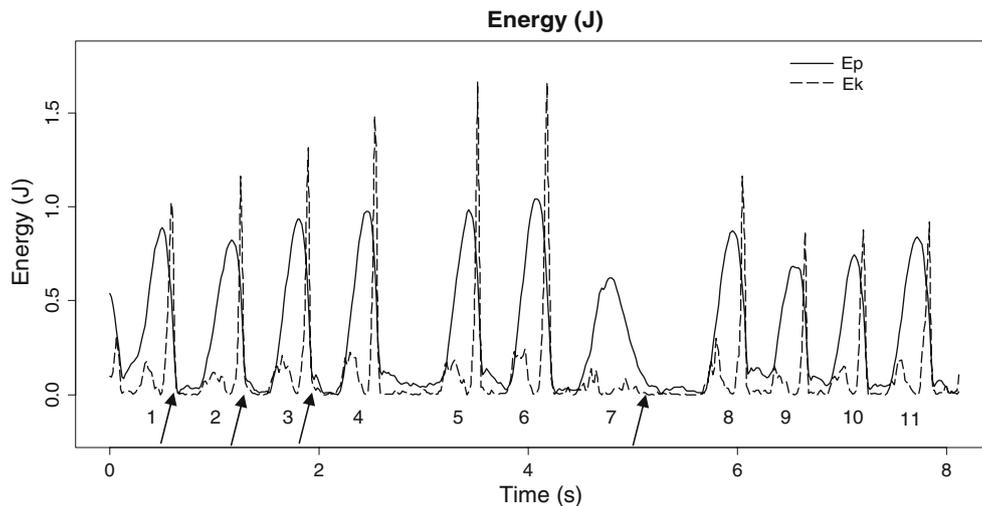


Fig. 4 Mechanical energy: hand + hammer potential (E_p) and kinematic (E_k) energy during a sequence of strikes to crack open macadamia nut on a stone anvil, computed for the light stone tool (0.327 kg) condition. The arrows mark the time of the hammer impact

each chimpanzee except that Misaki with the heavy hammer contributed for four nuts only.

From 380 strokes, 308 “functional strokes” were analysed, 148 for the light hammer (300 g) condition, 87 for the medium hammer (600 g) condition, and 73 for the heavy hammer (1,000 g) condition. For the individual stroke analysis, we excluded small amplitude strokes (strokes whose amplitude was less than half the larger stroke of the sequence) and small kinetic energy strokes (strokes whose kinetic energy was less than half the larger stroke of the sequence), as these strokes are being considered as not functional (as far as cracking the shell is considered). Figure 4 illustrates a sequence of strokes from the time series of potential and kinetic energy.

The average number of “functional strokes” to crack open a nut decreased with the hammer weight from 5.92 for the 300 g hammer to 3.48 for the 600 g hammer and to 3.05 for the 1,000 g hammer. However, large differences appear between chimpanzees. Loi produced respectively an average of 7, 3.6 and 1.8 for the 300, 600 and 1,000 g hammer, while for Zamba, the values were 2.6, 4 and 2.8 (see Fig. 5).

Mechanical energy computation: potential versus kinetic energy of the hammer

Table 2 shows the averaged results for the five parameters computed, i.e. amplitude of strokes, potential energy, velocity, kinetic energy and the ratio $r = E_k/E_p$ for the three hammer weight conditions and for each chimpanzee. Figure 5 shows the inter-individual and intra-individual differences for these same parameters.

Amplitude of the strokes The amplitude of the striking movement decreased with the weight of the hammer from an average of 11 cm with the 300 g hammer to 9 cm with

the 1,000 g hammer ($F_{2,293} = 9.172$, $P < 0.001$). The difference in amplitude was significant for the 600 and 1,000 g hammer comparison (Newman–Keuls, $P < 0.01$).

When looking at each chimpanzee individually, Mizuki produced significantly higher values of amplitude of the movement than all other chimpanzees and was the only one to display statistically significant differences between the three conditions. Loi produces higher values than the three other chimpanzees, but this difference is significant for the 300 g hammer condition only.

Potential energy (E_p) Potential energy increases linearly with the hammer weight, and is statistically different for each weight condition ($F_{2,293} = 221.8$, $P < 0.0001$). The average value is 0.61 J for the 300 g hammer, 0.86 J for the 600 g hammer and 1.15 J for the 1,000 g hammer.

All five chimpanzees displayed a very similar profile showing a statistically significant increased potential energy with the increasing weight of the hammer.

Loi and Mizuki displayed similar values for the three hammer conditions, higher than the value displayed by the three other chimpanzees.

Velocity at time of contact Velocity is greater for the 600 g hammer condition, with an average value of 2.12 m/s; significantly lower for the 300 g hammer condition (1.88 m/s) and for the 1,000 g condition (1.52 m/s).

All five chimpanzees produced a significant lower velocity for the 1,000 g hammer condition when compared with the 600 and 300 g hammer conditions. There is no difference in velocity when comparing the 600 and 300 g conditions, except for Tsubaki, who produced a significantly lower velocity for the 300 g hammer condition.

Kinetic energy The average kinetic energy varies significantly depending on the hammer condition ($F_{2,293} = 90.4$, $P < 0.001$). This difference is mainly due to the 300 g

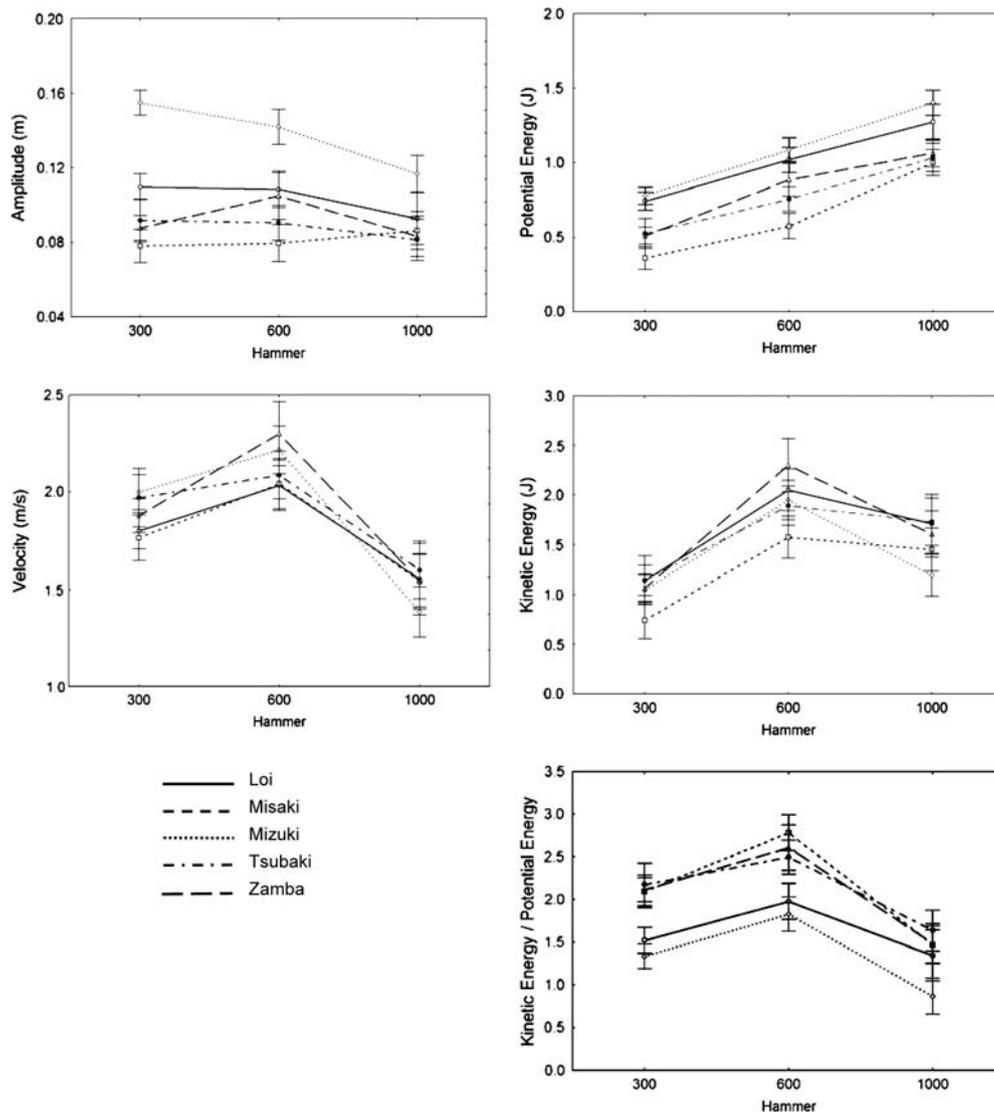


Fig. 5 Average values over the five chimpanzees for the stroke parameters for the three hammer conditions (300, 600 and 1,000 g): **a** amplitude, **b** potential energy, **c** velocity, **d** kinetic energy, **e** kinetic energy/potential energy ratio

hammer condition ($E_k = 1.04$ J). The average kinetic energy for the 600 g hammer condition and for the 1,000 g condition is equal to 1.92 and 1.50 J, respectively.

At an intra-individual level, there is no difference in kinetic energy when the 1,000 and 600 g hammer conditions are compared for Loi, Zamba and Misaki. Tsubaki and Mizuki produced lower kinetic energy in the 1,000 g hammer condition compared with the 600 g condition. All chimpanzees displayed significantly lower values for the 300 g condition compared to the 600 and 1,000 g hammer conditions, except for Mizuki who showed no difference between the 300 and 1,000 g hammer conditions.

Here again, the chimpanzees showed very little inter-individual differences in kinetic energy produced whatever the condition. Only Misaki produced significantly smaller value values in the 300 and 600 g condition.

Ratio $r(E_k/E_p)$ The mean values of the ratio r are significantly different ($F_{2,293} = 87.7$, $P < 0.0001$). They vary between 1.34 for the 1,000 g hammer condition and 2.31 for the 600 g hammer condition, the mean value for 300 g hammer condition is being 1.77.

All five chimpanzees have a significant lower value of r for the 1,000 g hammer condition compared with the 600 and 300 g condition.

An inter-individual comparison for each hammer condition shows that Loi and Mizuki displayed significantly lower values than the three other chimpanzees.

Sequences of strokes and strategy modelling

The analysis of the chimpanzees' strategies necessitates a minimum of three successive strikes. All together 71

Table 2 Mean (in bold characters) and standard deviation for all the parameters computed for all conditions

Chimp	Hammer	Nbr of strikes	Amp (m)	Amp Err-Ty.	E_p (J)	E_p Err-Ty.	Velocity (m/s)	Velocity Err-Ty.	E_k (J)	E_k Err-Ty.	r (E_p/E_k)	r Err-Ty.
Loi	300	35	0.1097	0.0036	0.7437	0.0308	1.799	0.0472	1.1418	0.0764	1.522	0.077
Loi	600	18	0.1084	0.005	1.0195	0.0429	2.035	0.0658	2.0510	0.1065	1.977	0.107
Loi	1,000	9	0.0926	0.0071	1.2737	0.0608	1.553	0.0931	1.7105	0.1506	1.344	0.1517
Misaki	300	22	0.0780	0.0045	0.3601	0.0389	1.763	0.0595	0.7447	0.0963	2.094	0.097
Misaki	600	18	0.0795	0.0050	0.5759	0.0429	2.042	0.0658	1.5757	0.1065	2.781	0.107
Misaki	1,000	17	0.0862	0.0051	1.0006	0.0442	1.544	0.0677	1.4504	0.1096	1.470	0.1105
Mizuki	300	38	0.1549	0.0034	0.7791	0.0296	1.999	0.0453	1.0491	0.0733	1.333	0.074
Mizuki	600	20	0.1418	0.0047	1.0866	0.0408	2.217	0.0625	1.9480	0.1010	1.828	0.101
Mizuki	1,000	18	0.1168	0.0050	1.4031	0.0430	1.386	0.0658	1.1932	0.1065	0.866	0.107
Tsubaki	300	40	0.0877	0.0034	0.5111	0.0289	1.8778	0.0442	1.0661	0.0714	2.113	0.072
Tsubaki	600	11	0.1047	0.0064	0.8853	0.0550	2.301	0.0842	2.3012	0.1362	2.608	0.137
Tsubaki	1,000	15	0.0831	0.0055	1.0649	0.0471	1.540	0.0721	1.6077	0.1167	1.486	0.117
Zamba	300	13	0.0916	0.0059	0.5251	0.0507	1.971	0.0775	1.1433	0.1253	2.174	0.126
Zamba	600	20	0.0903	0.0047	0.7553	0.0408	2.087	0.0625	1.8914	0.1010	2.496	0.101
Zamba	1,000	14	0.0813	0.0057	1.0334	0.0487	1.599	0.0746	1.7299	0.1208	1.637	0.121

Amp amplitude of striking movement, m metre, E_p potential energy, E_k kinetic energy, J joules, r ration E_p/E_k , m/s metres per second

sequences of three or more successive strikes were analysed, 18 for the 1,000 g hammer, 23 for the 600 g hammer and 30 for the 300 g hammer.

When considering sequences of three or more strikes, the average number of strikes per sequence decreased with the increase in the weight of the hammer. The mean sequence length was 3.89, 4.22 and 5.7 strikes for the 1,000, 600 and 300 g hammers, respectively.

Table 3 gives a summary of the results of the strategies when they significantly fit at least one model. When considering both potential and kinetic energies, more than two-thirds of the sequences could be modelled (note that a sequence of strikes may significantly fit more than one model). However, the proportion of sequences that respond

to none of the models is slightly larger in the 1,000 g hammer condition. The proportion of sequences that matched the first type of model [constant value and AR (2)] is smaller in the 300 g hammer condition than in the other two conditions. On the other hand, the number of sequences that matched the second type of models or “A priori knowledge models” (be it linear increment or 1st or 2nd order models, that corresponds to Eqs. 3, 4a, 4b) is larger in the 300 g hammer condition (Fig. 6).

Inter-individual differences are quite great. When considering the potential and kinetic energies, Loi and Zamba showed the largest number of sequences of strikes that fit at least one model of the second type. For these two individuals, when the sequence of potential energy fits one model, the sequence of kinetic energy fits the model as well. The other three chimpanzees displayed fewer sequences that significantly fit one of the three models of the second type.

Table 3 Proportion of sequences of strikes that statistically fitted one or several models when considering either potential or kinetic energy

Models	1,000 g hammer		600 g hammer		300 g hammer	
	E_p	E_k	E_p	E_k	E_p	E_k
<i>Blind strategy</i>						
No strategy	0.28	0.44	0.30	0.22	0.23	0.37
Eq. 1	0.06	0.11	0.22	0.17	0.20	0.03
Eq. 2	0.39	0.17	0.35	0.35	0.13	0.17
<i>A priori knowledge</i>						
Eq. 3	0.17	0.22	0.22	0.26	0.37	0.37
Eq. 4a	0.28	0.22	0.13	0.26	0.47	0.33
Eq. 4b	0.28	0.22	0.30	0.35	0.37	0.50

Models are grouped into *Blind strategy* and *A priori knowledge strategy* (see text for more details about the different models)

Discussion

A requirement for cracking a nut is producing the right amount of kinetic energy at the time of contact, so that the intact kernel can be released from the shell. Therefore, we consider that what has to be controlled is not the striking movement per se, but the energy transfer to the nut. The movement is then considered as the necessary support of the action that permits to reach this goal (Biryukova and Bril 2008). Referring to the studies on tool use from the ecological theoretical framework (Smitsman 1997), we

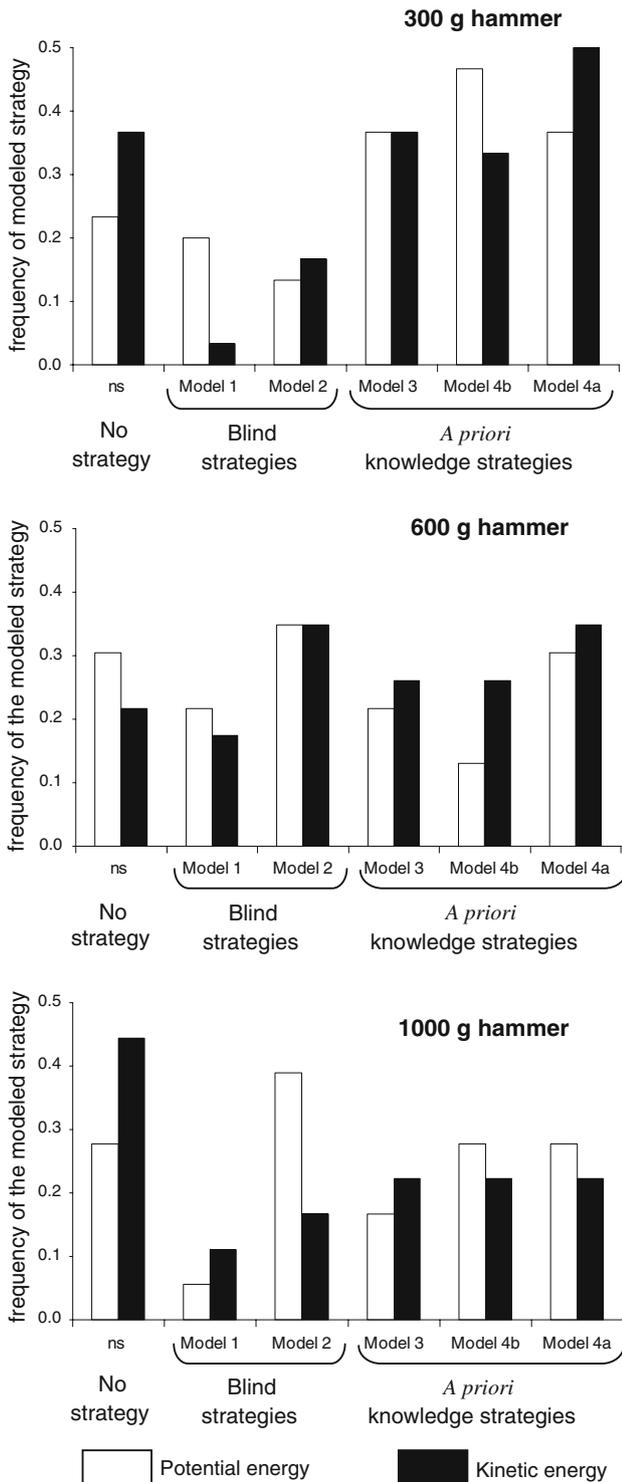


Fig. 6 Frequency of each type of sequence strategy for the three hammer conditions (none, “blind” or “A priori knowledge” strategies). Model 1: (Eq. 1) $S_n = M + \zeta$ Model 2: (Eq. 2) $S_{n+1} = \sum_{i=0}^{n-1} A_i S_{n-i} + \zeta$ Model 3: (Eq. 3) $S_n = A_0 + b \cdot n + \zeta$ Model 4a: (Eq. 4a) $S_n = A_0 + G \log(n + 1) + \zeta$ Model 4b: (Eq. 4b) $S_n = A_0 + a \frac{1+m e^{-n/\tau}}{1+n e^{-n/\tau}} + \zeta$

consider that the observed behaviour depends on how the chimpanzee handles many components of the task, and more specifically the dynamic interactions among gravity, hammer weight, amplitude of the strike, hardness of the nut, position of the nut and the anvil. Field studies have well established that chimpanzees are able to control this dynamic. The present study has investigated how a chimpanzee controls this dynamic. Two aspects of the task have been explored: the execution of a strike and the strategy developed by the chimpanzee in a sequence of strikes.

The control of energy transfer as a window on cognition

The results of the experiment clearly show that the five chimpanzees do adjust their strikes to the properties of the tool to crack open macadamia nuts, i.e. to produce an appropriate amount of kinetic energy at the time of contact. To adjust to the hammer characteristics, they simultaneously take advantage of the two possibilities that is they vary the amount of potential energy by varying the amplitude of the striking movement (Fig. 5) on the one hand, and by varying the kinetic energy of the hammer, through variation of velocity, on the other. The ratio $r (E_k/E_p)$ clearly shows that the chimpanzees do tune their muscular energy production depending on the weight of the hammer condition. In the 1,000 g hammer condition, they relied almost solely on potential energy to produce the right amount of kinetic energy. In the other two weight conditions, they produce 1.5–2.5 times more kinetic energy than just the transfer from potential energy.

Our hypothesis was that an optimal adaptation would give rise to the production of the same amount of kinetic energy, whatever the weight of the hammer be, as the functional demand of the task does not change, i.e. the nuts to crack open are all macadamia nuts (even though we probably over estimate the homogeneity of the nuts’ shells). The results partially confirm our hypothesis. Loi, Zamba and Misaki displayed the same kinetic energy in the 1,000 and 600 g hammer condition. This was not the case for Tsubaki and Mizuki who displayed a higher kinetic energy in the 600 g hammer condition. However, for these two chimpanzees the difference in kinetic energy produced in the 600 g and 1,000 g condition is much smaller than the difference observed between the 600 and 300 g conditions (see Fig. 5d).

The 300 g condition is interesting. In this case, all five chimpanzees produced significantly lower kinetic energy that in the two other conditions. This may be due to the impossibility of producing the right kinetic energy due to the excessively undersized weight of the hammer, which could not be compensated by the amplitude of the hammer trajectory or by the additional muscle energy produced, or

any combination of both. In most studies, stone hammers used by chimpanzees are usually much larger⁵. In addition, the size of the 300 g hammer could be too small to produce an effective hit because the size does not fit the chimpanzee's hand. The slightly higher value of kinetic energy produced in the 600 g hammer condition may be due to a better mastery of the situation owing to the chimpanzees' previous practice (prior to the experiment) that was mainly based on the 600 g hammer used in this experiment.

The behaviour of two of the five chimpanzees who participated in the experiment is worth further discussion as they clearly differ from the other three who displayed more similar behaviour. Mizuki, an 8-year-old female, produced significantly larger amplitude of her movement in all the three weight conditions, and consequently produced a much higher potential energy (Fig. 5a, b). A consequence of this strategy is a lower ratio E_k/E_p (see Fig. 5e), which means that Mizuki, once the position of the hammer is set up, will have to produce less muscular force to reach the same values of kinetic energy compared with the other chimpanzees. On the other hand, Loi, who is heavier, will produce the same potential energy from smaller amplitude of the striking movement. These examples clearly show the impact of the anthropometric characteristics of the body on the behavioural strategy to produce the necessary functional characteristics of the task.

Striking strategies

A look at the succession of strokes clearly indicates that the values of potential and kinetic energy of the sequence of strokes are not random. Approximately half of the sequences of three and more strikes do respond to one of the three "a priori knowledge" models. Among the sequences that did not fit any of these models, some were composed of a sequence of strokes of constant values of E_p and/or E_k . Others were apparently random. However, one question arises: what does it mean when a sequence of seven strikes offers a succession of four strikes, which deliver an increasing value of E_k , followed by three strikes delivering a much smaller value of E_k ? Such a sequence fits none of the models. Yet it may not be random at all. Here we face the real "nature" of the nut cracking activity. In fact, a sequence of strokes may relate to two different

goals: first, cracking the shell, and second, decorticating the nut to remove the kernel. Once the shell is cracked, this second phase necessitates much less kinetic energy. In our experiment, it was not possible to determine which stroke really had broken the shell. Therefore, we have probably underestimated the number of sequences responding to a controlled strategy.

The different models used suggest that when a strike parameter is clearly dependant on the previous strikes, this may result on different planning strategies. These strategies, that is the "dynamical solution" (Smitsman et al. 2005), may be very simple or more sophisticated and consequently reflect different levels of cognitive capacities (control). For example, the increase in kinetic energy observed may increase linearly, or the increase may be modulated and tend toward a value the chimpanzee has "planned in advance" (models 3, 4 and 5). This latter case indicates that the chimpanzee possesses some kind of "knowledge" of the end-state of the task that may be considered as a "model" of the task. Either knowledge of the force required to crack open macadamia nuts and/or knowledge that there is a limit to the hardness of the shell, and that it is necessary to reach this limit with increasing tuning.

Sequence organisation suggests that the final dynamics of the action (higher level) emerges from the constraints at a lower level (strikes) (Smitsman et al. 2005). The result of a strike depends on the attention to the many degrees of freedom (ddl) of the task that must be controlled.

There are two ways to increase the kinetic energy produced, either through an increase in potential energy via an increase in the amplitude of the strike or through an increase in velocity via muscle force. Looking at the 300 g hammer condition, it is interesting to note that 18 out of 30 sequences of strikes significantly fit one of the three "a priori knowledge" models for the potential energy, while this is the case for only 13 out of 30 when considering kinetic energy. Two very preliminary hypothetical interpretations could be given. As mentioned earlier, the 300 g hammer may be far too small to be compensated by muscular energy to produce the necessary increase in kinetic energy, even though the chimpanzees do "understand" the necessary increase in forces to crack open the nut. Here again, we may hypothesise the important role of experience. A comparison between Mizuki, the second youngest chimpanzee and Loi, the most expert chimpanzee, may illustrate this point. Five out of 16 Mizuki sequences of potential energy respond to one or more *a priori knowledge* models while the proportion is of 10 out of 14 for Loi. The figures are similar for kinetic energy though a bit lower (3 out of 16 and 8 out of 14 for Mizuki and Loi, respectively). These figures are not large enough to draw any conclusions, but they suggest a likely trend:

⁵ For example in a field experiment which took place in Bossou (Biro et al. 2003) the smallest stone hammers proposed to the chimpanzees to crack oil-palm, coula and panda nuts weighed 200 g, the largest weighing 5 kg. However, the study does not give the frequency of use of hammers depending on their weight. In another study, Boesch and Boesch reported that very few hammers less than 900 g were transported near the anvils. Anderson (1983) report use of 0.4–2.6 kg hammers in the Sapo forest. For Boesch et al. (1994) in the wild potential hammers weight ranges between 0.6 and 20 kg.

experience is an important dimension of controlled strategies (Hayashi et al. 2005).

Another aspect that characterises quite a few sequences of strikes is the repeatedly lower value of the first strike even when the sequences did not respond to any of the models tested. This behaviour may be interpreted as a necessary calibration of the dynamics of the hammer/arm/nut system (Bril et al. 2005). This first strike could be necessary to gather relevant information needed to regulate the forthcoming striking movements, that is, to adjust the forces to be produced by the striking movement necessary to crack open the nut (Warren 1991). This may appear as a typical perception-action cycle as proposed by Gibson (1986) “we must perceive in order to move, but we must also move in order to perceive” (p. 223).

Energy transfer as the control parameter

In this paper, we assume that any action producing movement (here a percussive movement) should be considered as a mechanical interaction with the external world. In terms of macroscopic physics, interactions are regarded as forces. In a goal-directed movement, producing the right amount of force by controlling energy is considered the control parameter.

However, the literature focuses mainly on the mechanism of arm movement control. Apart from the classical planning approach based on motor programs (Schmidt 1975), different models based on three main hypotheses commonly explain arm movement. The first hypothesis argues that the shape of the trajectory is what is controlled; the second one emphasises forces and torques as the origin of movement, and the last one suggests that the same mechanism controls posture and movement using a threshold.

Muscular forces could be interpreted as the result of an actuator, i.e. a linear (or angular) motor producing force (or torque). However, Hogan (1985) introduced a different point of view of how muscles are acting. The muscular system is not reduced to an actuator but rather to a visco-elastic mechanical system. Kinematics is produced by modifying the elastic and/or viscosity muscle parameter(s). In fact, these two parameters could be summarised in only one combined parameter called “impedance”.

Note that the purpose of most motor theories is to propose a general mechanism for arm movement regardless of the task at hand. Here, we propose a different perspective, departing not from a general principle but from the task constraints, i.e. a perspective based on energy production. Using an approach similar to Hogan’s (1985), we suggest that, in a goal-directed movement, impedance is used to adjust the energy transfer between kinetic and potential energy. From Hogan’s point of view,

kinetic energy produces trajectories depending only on impedance. We suggest here that for a goal-directed movement, part or all of this energy is needed to perform the task, i.e. to crack open a nut. In this case, the trajectory is an emerging property of the interaction between the task (and its constraints) and the organism. The functional aspect of the movement is the production of an accurate velocity to produce the right mechanical energy at the time of contact. We may assume that the control parameter is the mode of energy transfer during the movement, which corresponds to the production of dissipative energy. This parameter is related to muscular impedance and could be either negative (dissipative energy) or positive (additional energy). Therefore, we consider that what is controlled is the additional muscular force or torque (positive or negative) produced to change arm impedance during the movement.

For a specific action, once the tool has been chosen the potential energy could be directly controlled by setting up the initial arm position. Consequently, the kinetic energy at the point of contact depends on two parameters: potential energy (initial condition) and energy transfer control using dissipative energy. In almost all cases, the values of the kinetic energy/potential energy ratio were larger than one. This signifies that the chimpanzees were able to increase the total kinetic energy at the contact point, which means that they were able to produce additional energy using muscular control by modifying impedance. The analysis of the strategy revealed through the modelling of sequences of strokes reinforces this idea.

Conclusion

Field studies have reported many instances showing that chimpanzees successfully crack nuts. In the present study, our aim was to examine how the functional characteristics of the nut-cracking task are produced. This study, which should be considered as preliminary, establishes that primates’ capacities of adaptation are plainly revealed by the energetic parameters of movement (trajectories, velocity and kinetic energy). The data show that chimpanzees do mobilise passive (E_p) as well as active (muscular) forces to adapt to the task (changes in the weight of the tool), that is, to the dynamics of the arm/tool system. Our results suggest that the ability to determine the energetic constraints of the task, i.e. hence the ability to choose the right tools (here hammer and anvil) on the one hand (Foucart et al. 2005b), and to optimise the movement using energetic criteria, on the other is a marker into cognition. This approach offers a further means to “understand the basic causal principles that govern how objects interact with one another” (Povinelli 2000, p. 74). When an animal is acting in the real

world, it has to cope with a very specific and complex environment to satisfy its needs that is to exploit the possibilities to interact with and to manipulate its environment. How does the animal make use of its capacity to distinguish relevant from irrelevant properties of the tools at its disposal to act on its environment? In other words, the question is how does the animal capitalise on its cognitive capacities to achieve real-world goal-directed actions with the tools at hand? The functional approach to movement proposed here offers a way to develop further an analysis on situated or embodied cognition (Anderson 2003) that to some extent answers this question. In addition, it makes it possible to work out direct comparisons between human and non-human primates.

The large interest devoted to nut-cracking in chimpanzees is largely due to the relentless question of human specificity of tool use (Byrne 2005; Johnson-Frey 2003). Percussive activities in human and non-human primates have fed long-lasting and abundant debates on the development of human cognition. Percussive activity in early extinct hominins directed towards lithic production (Oldowan type) has been considered within the capacity of non-human primates (Wynn and McGrew 1989; Marchant and McGrew 2005). Questions concerning the capacity of great apes to produce highly controlled percussive movements contribute to the debates (Ambrose 2001; Roux and Bril 2005; Schick et al. 1999; Toth et al. 2006). The present results showing that chimpanzees are capable of adjusting the output of their movement to the properties of the tool in a way not very different from what is observed in humans (Foucart 2006, Bril and Foucart 2005) brings about the narrow range of differences between human and non-human primates.

Although this debate is beyond the scope of the present paper, the functional analysis of percussive activities proposed here may contribute to the discussion, as it can be developed in a similar manner in the area of stone-knapping activities (Biryukova and Bril 2008; Roux and Bril 2005). The level of analysis of percussive action proposed here considers movement as driven by the task constraints. Movements are analysed not for themselves, but as they generate the conditions of the task realisation. We believe that this level of analysis is critical in the understanding of primate adaptive behaviour.

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