An affordance analysis of unconditioned lever pressing in rats and hamsters[☆]

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ABSTRACT

Two experiments were conducted to assess the effect of lever height on lever pressing that was not explicitly reinforced – i.e., operant-level responding. Two rodent species were used as subjects, rats (Experiment 1) and hamsters (Experiment 2), aiming to compare the behavioral support offered by one lever at various heights relative to the subjects' body size. Results showed that lever height had a substantial effect on response rate. The rate of lever pressing varied similarly for rats and hamsters as a function of lever height, when lever height was re-scaled relative to body size. The distribution of inter-response times showed that lever pressing was organized in bouts separated by pauses. This pattern of responding was accurately described in both experiments by a mixture of two exponential distributions. These findings support an analysis of affordances in non-human species.

1. Introduction

Operant behavior is defined as responses that are emitted independently of preceding identifiable stimuli (Keller and Schoenfeld, 1950; Skinner, 1938). In other words, there is no particular stimulus that elicits operant behavior, or at least "no correlated stimulus can be detected upon occasions when it [the behavior] is observed to occur" (Skinner, 1938, p. 21). In order to be instrumentally conditioned, however, the operant must be emitted at least once. Responses emitted before conditioning are called *unconditioned* responses; the frequency or topography of an unconditioned response is the *operant level* of that response. It is presumed that unconditioned responses are part of the general activity of the organism (Baron et al., 1961; Keller and Schoenfeld, 1950).

Unfortunately, only a small number of experiments have systematically studied operant-level patterns of responding, and all of them were focused on lever pressing and carried out four to five decades ago (e.g., Bullock, 1950; Margulies, 1961; Segal, 1959;

Schoenfeld et al., 1950). The theoretical relevance of these patterns has been diminished and largely replaced by methodological concerns (e.g., its use as baseline performance to allow subjects to serve as their own control, to provide a basis to select subjects, etc.; Kiernan, 1965; Schoenfeld et al., 1950; Segal, 1959).

Some manipulations show ambiguous effects on operant-level rates of lever pressing, probably because of the very low frequencies typically observed. For example, manipulations of food deprivation and session length have revealed inconsistent results (Schoenfeld et al., 1950; Segal, 1959). Nonetheless, some regularities have been observed. It has been shown, for instance, that operant-level lever pressing increases with psychostimulants such as methamphetamine (Verhave, 1958; but see Verhave, 1958, Experiment 3). Also, more refined measures have shown that lever pressing is more forceful (Notterman, 1966), and of longer duration (Margulies, 1961) before conditioning than during conditioning (Notterman and Mintz, 1965).

Theoretical discussions about operant level are mostly focused on the strength of unconditioned responses and their relationship to the reflex reserve (Bullock, 1950). Keller and Schoenfeld (1950) suggested that an operant "must exist in some strength before conditioning" (p. 76); it therefore appears spontaneously with certain frequency and operates upon the environment to produce a consequence. Following Timberlake (2004), however, strictly speaking an operant is not developed before the contingency is established. An unconditioned response should be considered a 'proto-operant' or an 'operant candidate'; proto-operant responding by an organism confined into a chamber may be a behavioral component

of exploratory activity (Baron et al., 1961). Skinner (1938), for instance, noticed that rats often pressed the lever when they are exploring the wall above the lever.

Subjects in operant-level assessments often engage in exploratory activities, probably because these assessments are conducted in novel contexts (Bindra and Spinner, 1959). However, as context exposure increases, exploratory behavior and operant-level responding decline in frequency (Margulies, 1961; Schoenfeld et al., 1950; but see Baron et al., 1961; Segal, 1959). Recent research (Casarrubea et al., 2009) has shown that rodents confined in novel spaces show exploratory patterns that consist of rearing, followed by head scans, and then descent. During this behavioral sequence the forepaws are mainly used for postural support and to follow forequarter movements (Gharbawie et al., 2004; Schallert and Woodlee, 2005). Even in larger enclosures, rats engage in exploratory rearing. For example, Casarrubea et al. (2009) found that when rats were exposed to a 40 cm × 40 cm square arena, a high percentage of the exploratory behavior consisted of maintaining an erect posture, mostly leaning against the cage wall. Indeed, the rat's exploratory activities in the operant chamber can be facilitated by including a bar protruding from the wall. This protrusion could be a potential support for erected postures while leaning against the wall. If the surface of the lever is rigid enough and is high enough relative to the animal, then the lever may function not only as a surface to be explored, but it could also afford rearing behavior (see Gibson, 1966, 1979). This expectation is supported by recent experimental evidence that shows that exploratory activities in the object-exploration task are determined by the support afforded by the explored object (Chemero and Heyser, 2005, 2009; Heyser and Chemero, 2012).

Given these considerations, the present study was conducted to assess the effect of lever height on the frequency of operant-level lever pressing. We hypothesized that various lever heights provide differential postural support to rats and hamsters while exploring the chamber, and therefore the frequency with which the rat engages in unconditioned lever pressing and the duration of these engagements would differ with lever height.

2. Experiment 1: rats

2.1. Method

2.1.1. Subjects

Forty-two naïve male Wistar rats numbered RL01 to RL42 were obtained from the breeding colony of the University of Guadalajara. Rats were about 180 days old at the beginning of the experiment; their weights ranged from 340 g to 375 g. They were housed in individual cages (300 mm × 150 mm × 200 mm) located in a dimly lit room, and maintained on a 12-h/12-h light/dark schedule, with dawn at 8 h. Rats had free access to water; 13 g/day of solid food (Purina Chow) was available through the grid on the top side of the home cage.

2.1.2. Apparatus

A single 8-sided operant test chamber (MED® ENV-538) was used. The chamber was 340 mm high and 30.5 mm in span (the distance between parallel sides); each side was 120 mm long. The floor of the chamber was made of white polypropylene, the walls were aluminum sheets, and the top was made of clear polycarbonate. The chamber was equipped with a response lever (ENV-110M), 48 mm wide, protruding 10 mm into the chamber, that required a minimum of 0.2 N to operate. The tip of the lever had to be displaced 2 mm vertically to activate the switch. Switch activations were recorded every 0.1 s. The height of the lever from the floor varied across six conditions; it could be 30, 72, 114, 156, 198, or

240 mm. The chamber was located within a dimly lit-controlled room with white-noise to minimize environmental disturbances. Over the top of the chamber, a video camera (Sony® Handycam) recorded selected sessions to observe the topography of behavior.

In order to take body measurements of the subjects with all four limbs on the floor, a clear polycarbonate container (270 mm × 200 mm × 150 mm) was used. To take these measurements in vertical posture while maintaining contact with the floor only with the hind limbs, a clear polycarbonate cylinder, 300 mm high and 120 mm in diameter was used.

2.1.3. Experimental procedure

Twelve subjects were assigned to video recording sessions and 30 subjects to regular sessions. Subjects in regular sessions were randomly divided into 6 groups of 5 rats that varied in lever height (30, 72, 114, 156, 198, and 240 mm). To avoid potential confounds with time of day, one member of each group was randomly selected to constitute a squad. Each session began by placing the subject into the chamber, and ended 30 min later. Each rat was exposed to six sessions, and sessions were separated by approximately 48 h. All sessions were carried out during the light period. Feeding was conducted after the end of each session; on days without a session, feeding took place at about 2:00 PM.

Subjects in video recording sessions were divided into 6 pairs, each assigned to one of the lever heights used in regular sessions. Video recording sessions were similar to regular sessions, except that the top of the chamber was removed and only one session was conducted per rat. Data from one rat (lever height = 72 mm) were not used, because it escaped the chamber half way into the session.

After the completion of the experiment, the body size of regular-session subjects was measured in order to determine the maximum height at which each subject could press the lever, and the position of the lever relative to the subjects' body size. Each subject was placed into the clear polycarbonate container and was videotaped enough time to permit the exploration of the entire container (approximately 1.5–2 min). Subsequently, each subject was placed into the cylinder and videotaped. Four body dimensions were measured: (1) The maximum height of the subject's nose while rearing, (2) the maximum height of the forepaws while rearing, (3) the extension of the hind limbs when rearing, and (4) the maximum height of the subject's nose standing with the four paws on the floor (Fig. 1).

2.1.4. Data analysis 1: video recording sessions

Six 1-min samples of video recording were selected for each rat in video recording sessions. The first sample was the first minute of the session; the end of each sample was separated from the beginning of the next sample by 4 min. A naïve observer watched all samples and, using CowLog (Hänninen and Pastell, 2009), produced an ethogram with 5 behavioral classes: nosing wall (NW), vertical displacement (VD), horizontal displacement (HD), grooming and resting (GR), and lever exploration (LE). These classes are described in Table 1. Three dependent measures were obtained for each rat, each aggregated over the first 3 (early) and the last 3 (late) samples: (a) the proportion of time in each behavioral class, (b) the frequency (per min) of each behavioral class, and (c) the mean duration of each instance of the behavioral class (i.e., 60 s × proportion/frequency). A 2 × 2 mixed-design ANOVA was conducted on these dependent measures to identify significant effects of time in session (early vs. late) and height of lever (low: 30–114 mm vs. high: 156–240 mm).

2.1.5. Data analysis 2: regular sessions

The number of lever presses and latencies (the time elapsed since the beginning of the session to the first lever press) were averaged over sessions for each subject, and then across subjects within group. These served as dependent measures. A one-way ANOVA
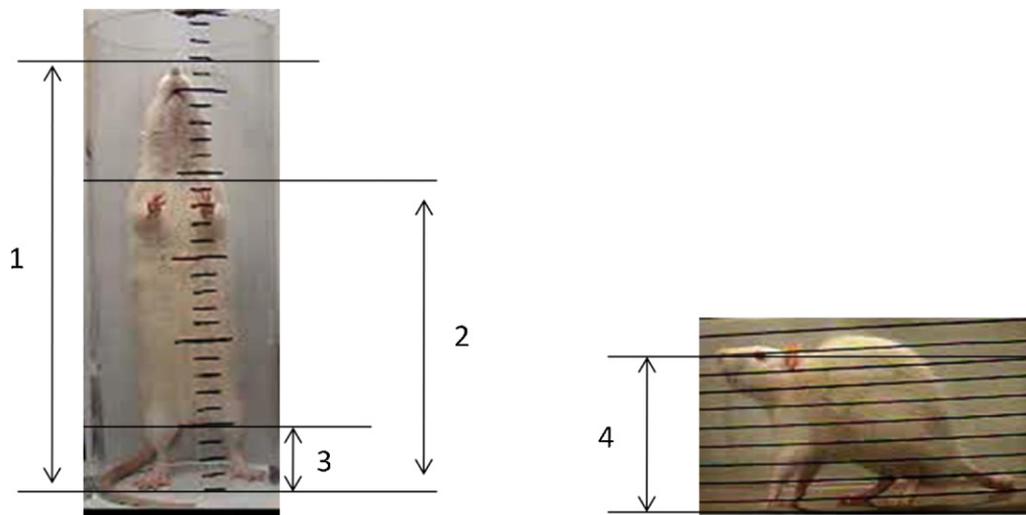
Fig. 1. The four body measures observed in the polycarbonate cylinder (left picture), and the container (right picture). (1) Maximum height of the subject's nose while rearing. (2) Maximum height of the forepaws while rearing. (3) Maximum extension of hind limbs. (4) Maximum height of the subject's nose standing with the four paws on the floor.

was employed to detect statistically significant differences in each dependent measure across lever heights. An unprotected confirmatory post hoc Fisher's LSD test was employed to identify pairwise differences in lever presses and latencies.

2.2. Results and discussion

Fig. 2 shows the analysis of video recording sessions. The frequency of and time spent in vertical displacements (VD), horizontal displacements (HD), and lever exploration (LE) significantly declined between the early and late parts of the video recording session (frequency of VD, HD, and LE, respectively: $F_{1,9} = 16.34$, $p = .003$; $F_{1,9} = 89.11$, $p < .001$; $F_{1,9} = 20.23$, $p = .001$; proportion of time in VD, HD, and LE, respectively: $F_{1,9} = 21.57$, $p = .001$; $F_{1,9} = 155.11$, $p < .001$; $F_{1,9} = 5.84$, $p = .039$). The frequency of nosing wall (NW) also declined over time in session ($F_{1,9} = 19.74$, $p = .002$). In contrast, the time spent grooming and resting (GR) and the duration of each instance of GR increased over time in session (respectively: $F_{1,9} = 26.02$, $p = .001$; $F_{1,9} = 6.80$, $p = .028$). When the lever was high, rats engaged in NW and HD more often (respectively: $F_{1,9} = 8.77$, $p = .016$; $F_{1,9} = 15.56$, $p = .003$), whereas LE declined in total time and frequency (respectively: $F_{1,9} = 16.73$, $p = .003$; $F_{1,9} = 6.64$, $p = .03$), relative to when the lever was low. No time in session × lever height interaction effect was detected.

The top-left panel of Fig. 3 shows the average number of lever presses as a function of lever height. Subjects exposed to the lever located at 30 and 156 mm from the floor responded, on average, more than any other group. Excluding the responses to the 30-mm lever, the responses were orderly distributed according to an inverted-U function, with maximum responding at the 156-mm

Table 1
Behavioral classes used in ethogram.

Class	Description
Nosing wall (NW)	Sniffing on wall (not lever) while all four paws are on the floor
Vertical displacement (VD)	Standing on hind legs with forepaws. May be leaning on wall, but not on lever
Horizontal displacement (HD)	Displacement by moving all paws on the floor
Grooming and resting (GR)	Any self-directed behavior, or absence of displacement with all paws on floor
Lever exploration (LE)	Sniffing, handling, leaning, or standing on lever

height and decreasing at lever heights of 198 mm and 114 mm; responses to the 240- and 72-mm high levers were the least frequent. A one-way analysis of variance (ANOVA) revealed a significant effect between groups ($F_{5,24} = 4.13$, $p = .008$). Confirmatory post hoc Fisher's LSD analysis showed that substantially more lever presses were made on the 30-mm and 156-mm high lever than on the 72- ($p = .002$ and .013, respectively) and 240-mm high levers ($p = .002$ and .011, respectively).

The bottom-left panel in Fig. 3 shows that the mean latency to the first lever press was longer for the groups where the lever was located at 30, 72, and 240 mm, whereas the group that responded to the lever located between 114 and 198 mm from the floor showed the shortest mean latency. A one-way ANOVA revealed significant differences between groups ($F_{5,24} = 3.18$, $p = .02$). A post hoc analysis showed that the mean latency to the first lever press was substantially shorter if the lever was 114-mm high than if it was 72-mm high ($p = .007$).

The four body measures of the rats obtained after completing the experiment are shown in the top panel of Fig. 4. Different symbols represent the average of maximum heights reached by rats for each body measure for each group. Across groups, subjects had similar body dimensions. The mean maximum height reached by the subjects from the extreme of the hind limbs to the nose (filled circles) while head scanning the top of the cylinder was 245 mm. The mean maximum height reached from the hind limbs to the forepaws while wall exploring was 184 mm (open circles). The mean maximum height of the subjects' nose while they maintained contact with the container floor with all four limbs was 113 mm (filled triangles), and the mean extension of the hind limbs when rearing was 53 mm (open triangles).

The top panel of Fig. 4 also shows that the highest lever position was close to the maximum measure of body from hind limbs to the nose (filled circles). The maximum height reached from the hind limbs to the forepaws while rearing (open circles) was slightly below the 198-mm lever, but above the 156-mm lever. The maximum height of the subjects' nose while they maintained contact with the floor with all four limbs (filled triangles) matched the 114-mm lever. Finally, the maximum extension of the hind limbs (open triangles) was higher than the 30-mm lever.

2.2.1. Modeling the lever's affordance of pressing behavior

It may be expected that, similarly to reinforced lever pressing, the intervals between operant-level lever presses are organized
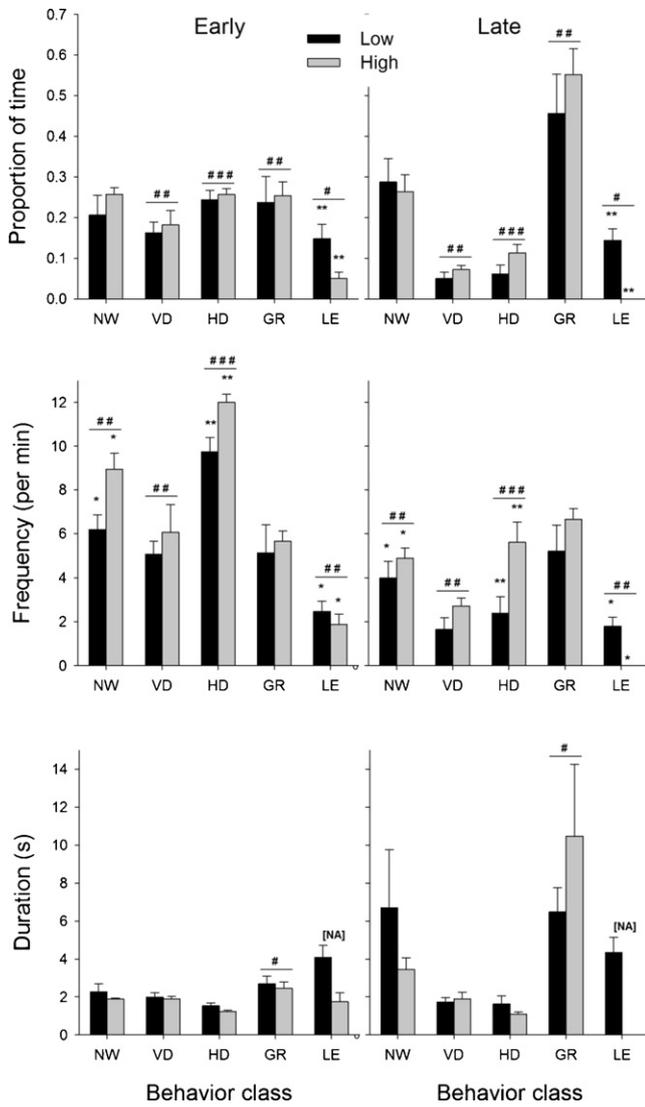
Fig. 2. Analysis of video recording sessions. Proportion of time (upper panel), frequency (middle panel), and mean duration (lower panel) for each behavioral class, in early (first 15 min; left panels) and late (last 15 min; right panels) session periods. Black bars correspond to levers located at low heights (30–114 mm); gray bars correspond to lever located at higher heights (156–240 mm). NW: nosing wall; VD: vertical displacement; HD: horizontal displacement; GR: grooming and resting; LE: lever exploration. Pound symbols (#) indicate significant main effects of time in session (early vs. late); asterisks (*) indicate significant main effects of lever height (low vs. high). One symbol is $p < .05$; two symbols is $p < .01$; three symbols is $p < .001$.

into bouts of activity separated by pauses (Shull and Grimes, 2003; Brackney et al., 2011; Cheung et al., 2012; Hill et al., 2012). This expectation derives from two premises: (1) experimental evidence shows that exploratory behavior is organized into bouts of lateral and vertical scans where forepaws are used for postural support (Gharbawie et al., 2004), and (2) the lever provides postural support while the rat explores the chamber, and such postural support as an opportunity to wall and top exploration is reinforcing (Hughes, 1997), beside from the reinforcing effect of manipulating the lever (Kish and Barnes, 1961). Lever pressing in bouts may result from frequent lever activations while top scanning and wall exploring, separated by relatively long pauses when the subject performs other activities such as locomotion and grooming (Shull et al., 2001). Assuming this pattern of responding, the opportunities for lever pressing, and therefore the lever's capacity to afford pressing, could be revealed by the frequency with which the rat initiates a

bout, the duration of those bouts, and the speed at which the lever is pressed within each bout.

Using a log-survival analysis, Shull et al. (2001) found that the distribution of inter-response times (IRTs) could be accurately described as a mixture of two exponential distributions, one consisting of short IRTs, and the other consisting of longer IRTs. Brackney et al. (2011) added the assumption that IRTs below a minimum duration are not possible, and applied the method of maximum likelihood estimation (MLE) to estimate parameter values. Brackney and colleagues' bi-exponential refractory model expresses the probability density of an IRT as:

$$\text{If } \tau < \delta, \ p(\text{IRT} = \tau) = 0$$
$$\text{If } \tau \geq \delta, \ p(\text{IRT} = \tau) = (1-q)we^{-w(\tau-\delta)} + qbe^{-b(\tau-\delta)}, \quad (1)$$

where δ is the minimum IRT, w is the mean within-bout response rate, b is the mean bout-initiation rate, and q is the probability of quitting a bout after a response (i.e., the proportion of IRTs that separate bouts). The mean bout length, measured in lever presses, is the reciprocal of q, $1/q$. The mean bout duration, measured in time, is $(1/q)(1/w+\delta)$. It is important to note that response latency – the time to the first lever press in the session – is not counted as an IRT.

Fig. 5 shows the log-survivor plots of IRTs pooled across rats within each lever height condition. The diamonds are the observed proportion of IRTs greater than τ; the solid light lines are fitted traces of Eq. (1). Fits were carried out by setting δ as the empirical minimum IRT ($\delta = 0.1$ s in all conditions, except in the 240-mm condition, where $\delta = 0.2$ s; note that the temporal resolution for recording lever presses was 0.1 s). Then, MLE was implemented using the Solver add-in in Microsoft Excel for Windows 2008, and applied to estimate w, b, and q.

One notable feature in Fig. 5 is the sharp inflection in the log-survival plot, falling steeply at first and then more gradually. This is the typical broken-stick appearance observed in reinforced responding (Shull et al., 2001). The slope of the initial limb is the within-bout response rate (w); the slope of the second limb is the bout-initiation rate (b). This broken-stick pattern is an indication that lever pressing was organized in bouts,[3] as described in Eq. (1). A straight log-survival plot would have indicated a constant rate of lever pressing; multiple inflections in the log-survival plot would have indicated multiple classes of bouts, each with a distinct mean response rate.

Table 2 summarizes the estimates of parameters from Eq. (1) (rats column) within each lever height. Table 2 shows that the probability of quitting a bout (q) is higher at those lever heights with fewer responses (72 and 240-mm; cf. Fig. 3, top-left panel), whereas the bout initiation rate (b) was higher for three out of the four lever heights that maintained more responding (30, 156, and 198-mm). No consistent tendency was found for the within-bout response rate (w). An analysis based on Akaike Information Criterion (AIC), showed that differences in parameters between lever-height conditions were likely to reflect changes in the process that generated the data, and not just sampling variance (Appendix A).

Consistent with our hypothesis, the frequency and duration of lever engagements differed with lever height. Moreover, the frequency of these engagements changed over time in session. These effects may explain important features of unconditioned lever pressing. Overall, lever exploration declined over time in session (see Margulies, 1961; Schoenfeld et al., 1950), along with various other exploratory behaviors (nosing, vertical and horizontal displacements), suggesting that lever contacts are part of the

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[3] Or that rats were lever pressing at a constant rate, but one group of rats was pressing very fast and the other was pressing much slower. Examination of the distribution of rates of lever pressing among rats rules out this possibility.
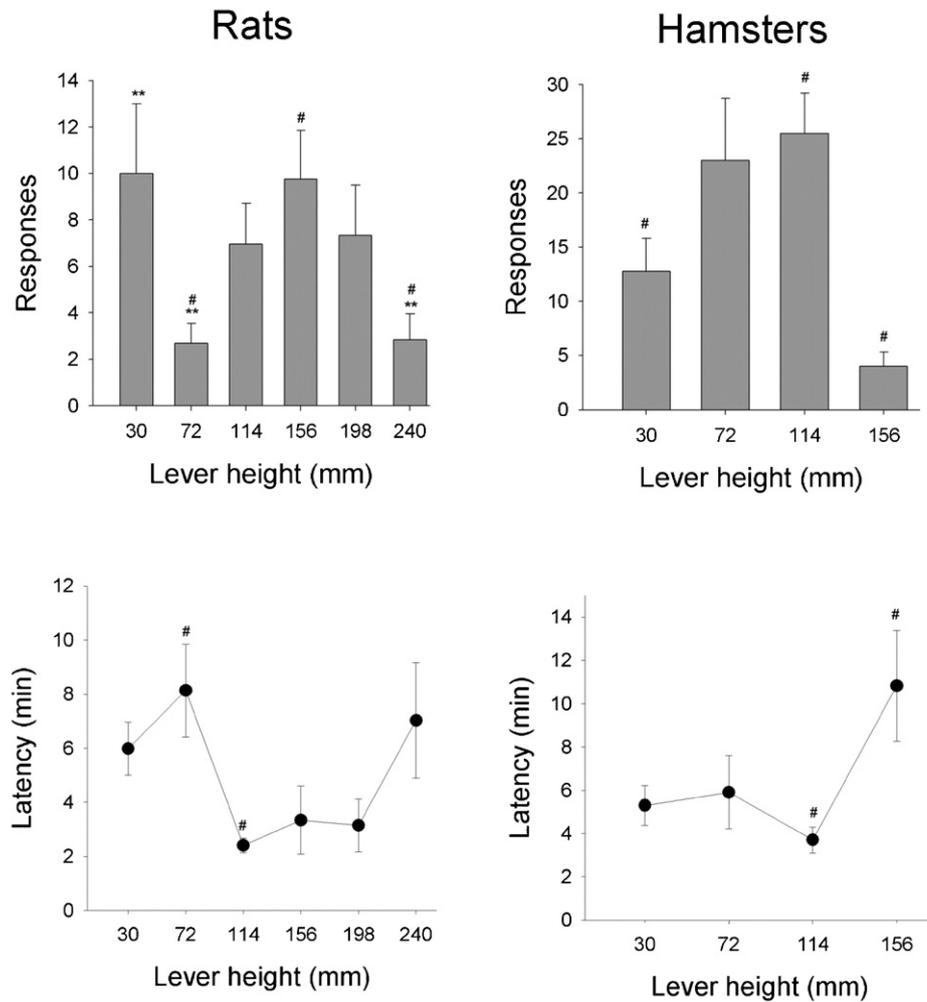
Fig. 3. Mean (±SEM) lever pressing by rats (top left panel) and hamsters (top right panel) as a function of the lever height, and mean (±SEM) latency to the first lever press for rats (bottom left panel) and for hamsters (bottom right panel). Symbols indicate significant differences ($p < .05$) between specific levels of each independent variable.

exploratory behavior of the rat, probably elicited by the novelty of the chamber environment. When the lever was at least 156-mm high, lever exploration was rare; instead, rats engaged significantly more often in nosing and horizontal displacement activities. This suggests that wall exploration and locomotion might have been substituted with lever exploration, when the lever was not too high.

The latency to the first lever press and the frequency of lever pressing (Fig. 3, left panels) provide additional details on the role of the lever during exploratory behavior. Short latencies at intermediate lever heights (114–198 mm) are consistent with the notion that early exploratory behavior was directed to a particular vertical spatial range. The late but highly frequent pressing at the lowest lever (30 mm), suggest that, unlike lever pressing at other heights,

this activity was not related to exploratory behavior but rather to resting, which increased in duration over time in session (Fig. 2).

The organization of unconditioned lever pressing in bouts provides further details on behavior directed toward the lever. When the lever was very low, or separated from the floor by about the same distance between hind limbs and forepaws, rats engaged the lever frequently (high b), emitting fast (high w) but relatively short bursts of pressing. This pattern of behavior on very low levers may be related to post-exploratory behavior, as discussed above. On higher levers, these frequent-fast-short bursts of lever pressing may reflect the support provided by the lever for wall exploration. Thus, the distance between the hind limbs and the forepaws may be the optimal height for the location of objects that support top scanning and wall exploration, which is

Table 2
Estimates of the bi-exponential refractory parameters (Eq. (1)) for rats (Experiment 1) and hamsters (Experiment 2).

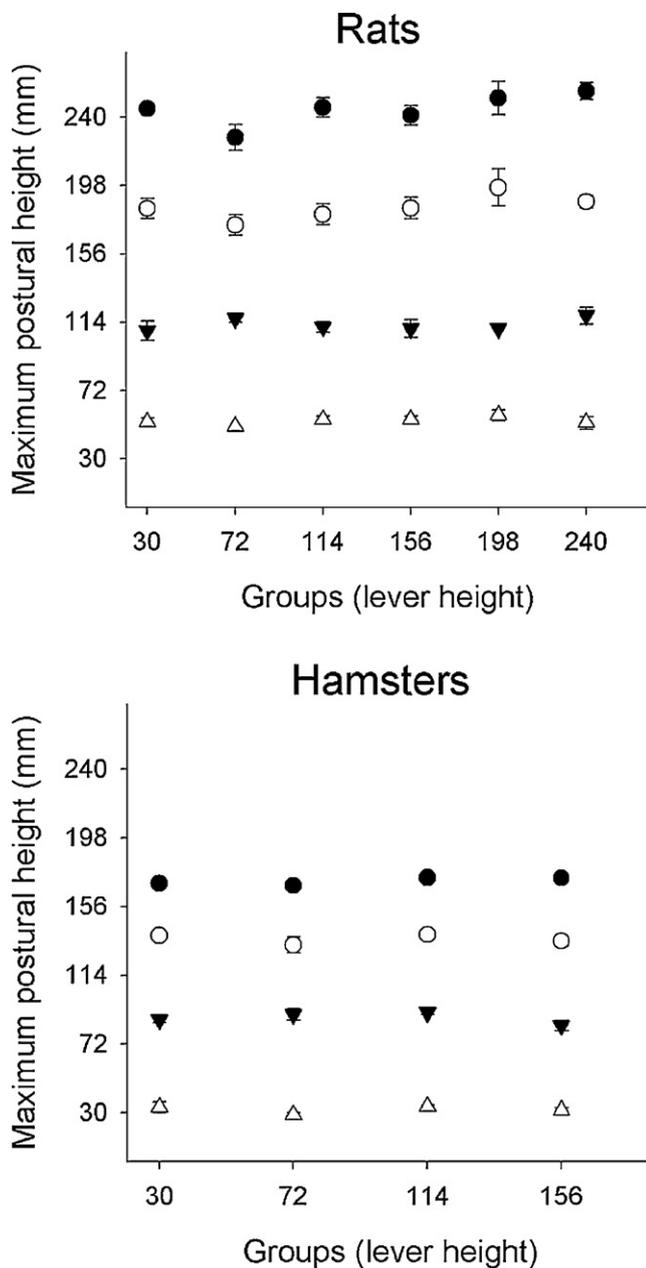| Lever height (mm)	Rats			Hamsters		
	q	b (resp/h)	w (resp/h)	q	b (resp/h)	w (resp/h)
30	0.34	24.92	2026.61	0.56	32.27	1638.19
72	0.60	11.58	1184.48	0.38	30.49	1063.77
114	0.35	11.51	713.60	0.33	26.40	1156.09
156	0.48	17.62	1264.97	0.43	17.57	1020.88
198	0.47	20.61	1423.27	–	–	–
240	0.60	11.13	1558.95	–	–	–

Fig. 4. Four body measures of rats (left panel) and hamsters (right panel): the maximum average height reached by the subjects from the extreme of the hind limbs to the nose (filled circles), the maximum average height reached from the hind limbs to the forepaws (open circles), maximum height of the subjects' nose while they maintained contact with the container floor with all four limbs (filled triangles), and the maximum extension of the hind limbs when rearing (open triangles).

expressed as frequent, rapid, but short contacts with those objects. The pattern of lever activation at intermediate lever height (around 114 mm, or 0.6 of hind-to-forelimb distance) was very different. Bouts of lever pressing at these heights were rare, slow, but very long in duration. This difference may be related to the distinct behavior class supported by each lever: at the hind-to-forelimb height the lever may support top scanning and wall exploration; at nose height it may support exploration closer to the floor, which may be expressed as infrequent but long bouts of scattered lever pressing.

3. Experiment 2: hamsters

Gibson (1979) suggested that those objects that afford an action have to be measured relative to the animal size, that is, by a body-scaled metric or intrinsic metric (Warren, 1984, 1995), rather than an extrinsic metric (i.e., a metric independent to the organism body-size). In Experiment 1 we showed that lever pressing in rats could be reliable described by the q, b, and w parameters from the bi-exponential model, assuming a two-mode response rate (Shull et al., 2001) in an operant-level setting. Experiment 2 had two purposes: (1) evaluate if the body-scaled metric of lever height determined the frequency and distribution of lever pressing, and (2) determine if the bi-exponential model accurately describes operant-level responding using different rodent species. Hamsters served as subjects, because they are smaller than rats, but are heavy and strong enough to press a lever designed for rats (Anderson and Shettleworth, 1977; Lea and Tarpy, 1986).

3.1. Method

3.1.1. Subjects

Fourteen naïve male golden hamsters (numbered HL01 to HL14) were obtained from the breeding colony of the University of Guadalajara. Hamsters were about 120 days old at the beginning of the experiment, and their weights ranged from 98 g to 104 g. They were housed in individual cages (27 cm × 20 cm × 15 cm) located in a dimly lit room, and maintained on a 12-h/12-h light/dark schedule, with dawn at 8 h. During the experiment, hamsters had free access to food (about 8–9 g/day Purina Chow) and water available through the grid on the top side of the home cage.

3.1.2. Apparatus

The same octagonal chamber described in Experiment 1 was used, with the exception that only four lever heights were used: 30, 72, 114, 156 mm. Body measures were taken using the same container and cylinder described in Experiment 1.

3.1.3. Procedure

Subjects were randomly divided in four groups according to each lever height (30, 72, 114, and 156 mm). Four subjects were assigned to groups of 30 and 72 mm lever height, and three subjects were assigned to groups of 114 and 156 mm lever height. Behavioral procedures and data analysis were the same as in Experiment 1, with the exception of video recording in the presence of a lever, which was not conducted in the current experiment.

3.1.4. Data analysis

Data were analyzed as described for the regular sessions in Experiment 1.

3.2. Results and discussion

The top-right panel of Fig. 3 shows the frequency of responding as a function of lever height. The one-way ANOVA revealed significant differences between groups ($F_{3,10} = 4.64$, $p = .028$). The confirmatory Fisher's post hoc analysis demonstrated that, on average, hamsters responded substantially more to the 114-mm high lever than to the 30-mm high lever and the 156-mm high lever.

The bottom-right panel of Fig. 3 shows the latency to the first lever press as a function of lever height. Hamsters took the most time to emit the first response when the lever was located at 156 mm, and the least time when located at 114 mm. The one-way ANOVA showed no significant differences between groups ($F_{3,10} = 3.25$, $p = .07$). Confirmatory Fisher's post hoc test showed a significant difference between the 114 and 156 mm lever height ($p = .013$).
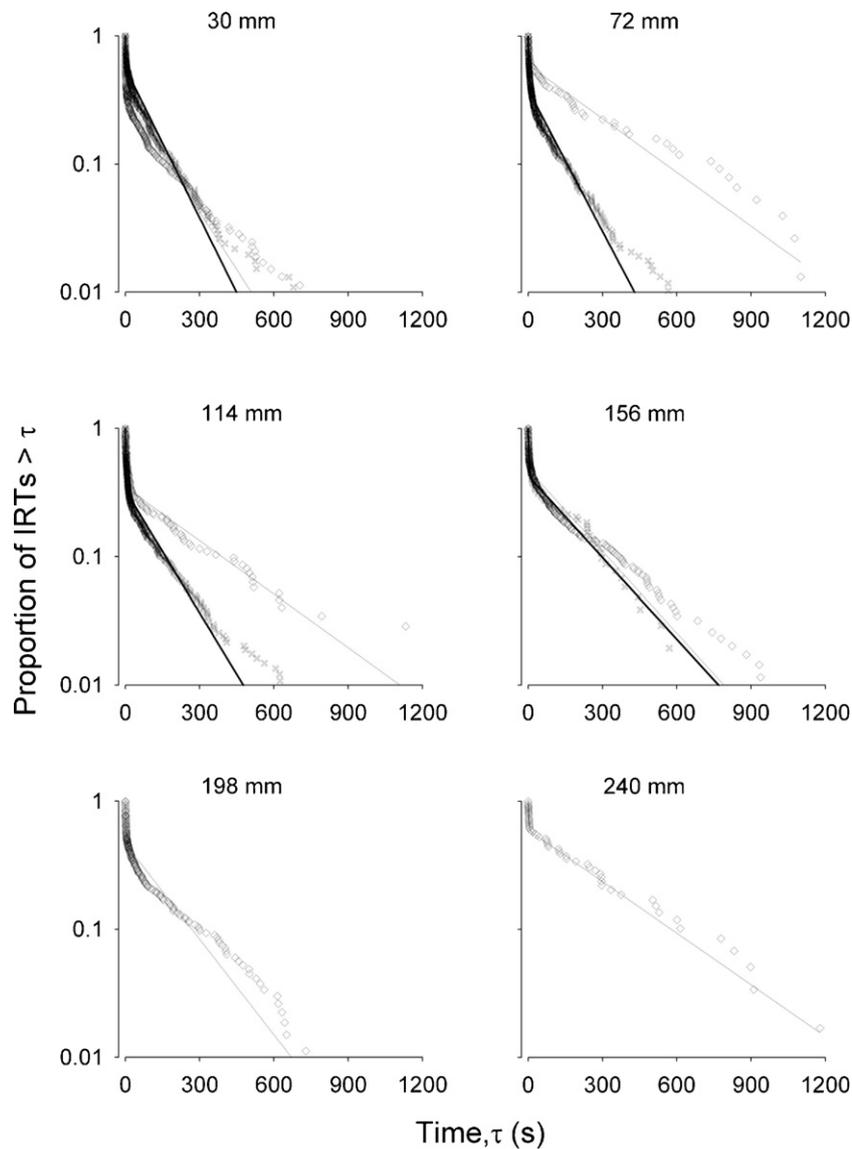
Fig. 5. Log-survivor plots for each lever height in Experiment 1 (diamonds and light solid lines) and Experiment 2 ('x' symbols and heavy lines). Diamonds and 'x' symbols represent the frequency distribution of IRTs; solid lines are fitted traces of Eq. (1). Each panel corresponds to a different lever height.

The four body measures of hamsters are shown in the bottom panel of Fig. 4. The maximum height from hind limbs to forepaws while rearing (open circles) was slightly below the 156 mm lever height (the maximum size from the hind limbs to nose while rearing was 172 mm, see filled circles), and slightly above the 114 mm lever height. The average maximum nose height with all four limbs on the floor was 88.2 mm (filled triangles), slightly above the 72-mm lever height. Finally, the maximum extension of the hind limbs (open triangles) matched the 30 mm lever height.

Fig. 5 ('x' symbols and heavy lines) shows the log-survivor IRT plots for each lever height (first four panels). Across all four lever heights, the log-survivor plots followed a broken-stick shape, which is consistent with the bi-exponential model of IRT distribution (Eq. (1)). Table 2 (hamsters column) summarizes the parameter estimates for Eq. (1). The probability of quitting a bout (q) was higher at those lever heights with fewer responses (30 and 156-mm), whereas the bout initiation rate (b) was low only for the lever height with fewer responses emitted (156-mm), and invariant for the other lever heights. Finally, no

consistent tendency was found for the within-bout response rate (w).

3.2.1. Affordance analysis of lever pressing

Warren (1984, 1995) proposed a dimensionless analysis to describe the fit between environment properties and organism activity. This analysis was named *intrinsic metric* because it considers the metric of the environment in relation to the body dimensions and biodynamic capabilities of the organism, in contrast with *extrinsic metric* where measures are specified independently of the body dimensions of organisms. Thus the intrinsic metric (also known as π numbers) can be defined as the ratio of the object's dimension with respect to the organism's dimension:

$$\pi = \frac{E_d}{O_d} \tag{2}$$

where E_d represents one environmental property and O_d represents one organism property. The intrinsic metric allows finding both, the maximum distance reached by an organism (the *absolute critical*
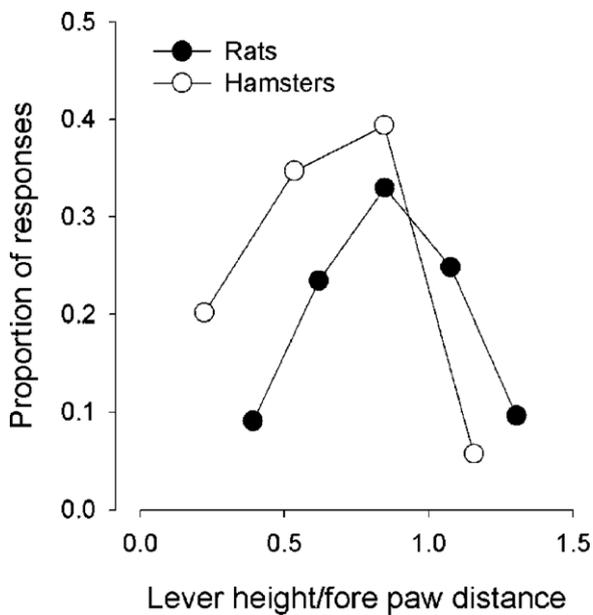
Fig. 6. Proportion of responses (rats, filled circles; hamsters, open circles), as a function of the ratio of lever height over the distance from hind limbs to the forepaws.

boundary) and the optimal point or *preferred critical boundary* at which an action will be better performed (Mark et al., 1997).

To analyze the lever pressing of rats and hamsters following an intrinsic metric, we first considered the maximum height reached from the hind limbs to the forepaws while rearing (Fig. 1) as the organism's dimension (O_d). The height of the lever served as the object's dimension (E_d; for the rats, the 30-mm high lever was excluded in order to compare data of rats with hamsters). Fig. 6 shows the proportion of responses of rats (filled circles) and hamsters (open circles) as a function of the ratio of lever height over the distance from hind limbs to the forepaws (intrinsic metric function or π). It is evident that lever pressing for rats and hamsters matched just below 1.0, where more lever pressing was emitted by both species. In other words, subjects responded more frequently at the same lever height relative to their body dimensions. This finding is consistent with affordance analyses performed on humans (e.g., Warren, 1984, 1995).

To evaluate if the estimates of the parameters of the bi-exponential model (Table 2) matched between rats and hamsters using the intrinsic metric, Fig. 7 shows the parameters summarized in Table 2 for rats (filled circles) and hamsters (open circles) as a function of the distance from hind limbs to the forepaws. Note that the unconnected filled circles (rats) did not have a corresponding lever height/animal size ratio for hamsters (open circles). Estimates of q (panel A), the probability of quitting a bout after a response, indicate that, excluding $\pi = 0.2$ (unconnected circle), in general rats and hamsters showed a bitonic U-shaped function. Estimates of b, the bout-initiation rate (panel B), show no systematic pattern for rats and hamsters, except for the decrease at the higher lever height. The estimate of w (panel C) for the hamsters was not as systematic as it was for rats, which had the lowest estimate at 0.6 (V-shaped), nevertheless, the first three values (from 0.2 to 0.8) paralleled closely the rats' pattern. Finally, the mean bout duration (panel D) changed more extremely for rats than for hamsters at $\pi = 0.6$, even when the global pattern was similar.

In general, the results indicated that rats and hamsters decreased lever pressing as lever height differed from the distance between hind limbs and forepaws (see inverted U-shape, Fig. 6). In both species, this pattern of change in response rate appears

to be linked to primarily to changes in the probability of quitting response bouts.

4. General discussion

Two main findings were derived from both experiments: In operant-level conditions (a) the height of the lever, relative to body dimensions, is an important feature that controls response rate, and (b) lever pressing is organized into bouts separated by pauses, described by the bi-exponential model (Eq. (1)).

Concerning the first finding, when scaling the environmental properties relative to the body size of subjects (i.e., intrinsic metric formulated in Eq. (2) and represented in Fig. 6), similar response-frequency profiles were obtained in rats and hamsters. Specifically, when the lever was located slightly below the maximum height of forepaws of rats and hamsters, the lever supported more responding than at other heights. The maximum limbs' height or distance reached by an organism is known as the *absolute critical boundary* (Warren, 1984); nevertheless, the *preferred critical boundary* defines the more comfortable mode of action, and is shorter than the absolute critical boundary (Mark et al., 1997; Stasik and Mark, 2005). In our results, because the 156-mm lever height for rats and the 114-mm lever-height for hamsters supported more responses, and because they were slightly below the maximum height that subjects could reach with their forepaws, they may represent the preferred critical boundaries or most comfortable lever positions for subjects to place their forepaws while exploring walls.

The high frequency of responses emitted by the rats to the 30-mm high lever could be explained by the variety of topographies through which the subjects could contact the lever, including pressing with the hind limbs. No equivalent lever height relative to the hamsters' body size was used; therefore, this response pattern was not found in hamsters.

In relation to the second finding, a fine-grained IRT analysis revealed that lever pressing was organized into bouts, similarly to reinforced responding (Shull, 2004; Shull et al., 2001, 2002). Research has shown that bout-initiation rate depends on rate of reinforcement, deprivation level (Shull, 2004), and effort requirement (Brackney et al., 2011), whereas within-bout responding depends on schedule demands. Since no primary reinforcement such as food or water was used in our experiments, the organization of responses into bouts could be described as the result of the behavioral support that the lever offered to the subjects when engaged in exploratory activities. In other words, as the subjects explored the chamber, the lever located at different heights afforded different behaviors and postures relative to their body structure and dimensions. Both main findings of the present experiments suggest that operant-level responding could be described as the result of affordances that the operant environment offers to the subjects, such as limb placing, biting or even "sitting".

The possibility that the rat presses the lever while exploring the wall above the lever was first identified by Skinner (1938) as a problem that he tried to correct.[4] Nevertheless, Skinner quoted Tolman (1932) to remark that any behavior requires an 'external support', given that it cannot occur in vacuo, and the "response must act upon the environment to produce its own reinforcement" (Skinner, 1938, p. 50). Therefore, the lever constituted an external support for responding (see Timberlake, 2004) even before conditioning, given the repertoire of niche-related behaviors it affords

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[4] Skinner (1938) noticed that rats often pressed the lever while exploring the top of their cages. For Skinner, this constituted a confounding behavior when measuring the strength of the lever-pressing response. To minimize exploratory lever presses, he mounted a screen just above the lever.
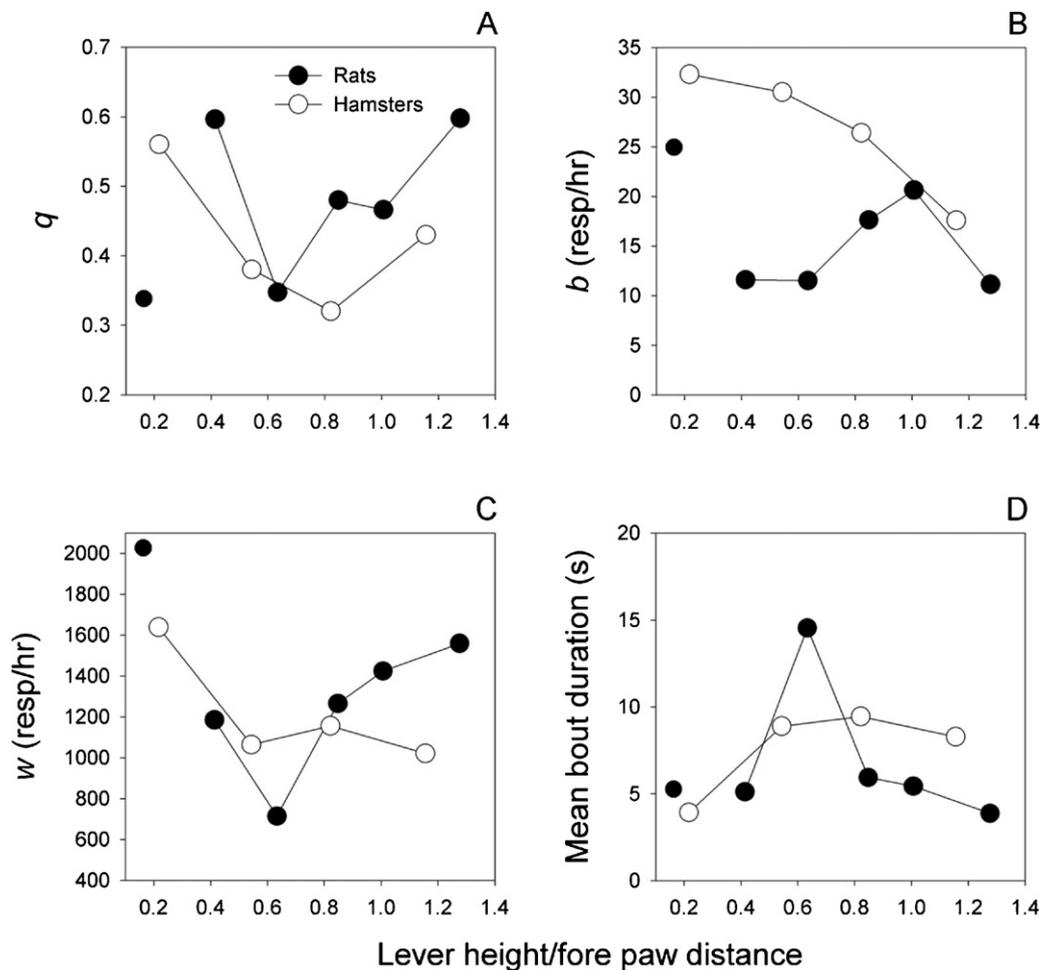
Fig. 7. Estimates of parameters of the bi-exponential refractory model (Eq. (1)) as a function of re-scaled lever height in rats (filled circles) and hamsters (open circles). Lever height was re-scaled by dividing it by the mean distance between hind limbs and forepaws in each species.

such as rearing and investigating (Timberlake, 2001). The external support for behavior is deliberately 'tuned' by the experimenter relative to the organism size, structure and biomechanical properties in order to facilitate responding and "enhance the vigor and reliability of responding" (Timberlake, 2001, p. 86).

In general, the results of the present experiments suggest that the emission of unconditioned responses is dependent on both the animal properties (body scale and biomechanics) and the surfaces surrounding the animal. When the layout of the surfaces matches the body scale of a given posture of the organism (i.e., there is organism–environment reciprocity), a pattern of action is engendered. This pattern of action could be formalized through the bi-exponential model (Eq. (1)), differentiating three particular features of unconditioned activities: bout initiation, within-bout responding, and probability of quitting a bout.

4.1. Relevance for human studies

When analyzed using the notion of the affordances, operant level responding parallels the behavior of children when coping with novel objects and surfaces (Gibson and Pick, 2000; Tonneau et al., 2004). Just as non-human animals explore and identify the surfaces that could serve as support for some activities (Chemero and Heyser, 2009; Heyser and Chemero, 2012), children learn the environmental supports for action by engaging in investigative activities (Gibson, 1988)

because "learning about affordances entails exploratory activities" (p. 5).

Several studies with humans also provide evidence that modes and patterns of action adjust accordingly to changes in the affordances and layout of the environment (Mark et al., 1997; Lopestri-Goodman et al., 2009; Warren and Whang, 1987) and by anthropometric and biomechanic restrictions (Cesari and Newell, 2000a,b; Chang et al., 2009; Newell et al., 1993). There are, however, limits to these adjustments. These limits are named *absolute critical boundaries*; they indicate that the relationship between an actor's capabilities and the properties of the environment supporting a specific mode of action changes at particular body–environment scaling invariants (Warren, 1984). For example, the limit at which the length of the legs of a person allow bipedal climbing to pass a step while walking or stair climbing (Konczak et al., 1992; Warren, 1984). Based on some of these findings in human performance, some authors have proposed the potential usefulness of the affordance analysis for the field of ergonomics to approach the scaling problems that the design of workplaces raises (Choi et al., 2007; Dainoff et al., 1999). In our experiments, the body size, body structure, and biomechanic constraints of subjects determined the frequency, distribution, and topography of lever pressing. The *absolute critical boundaries* for reaching the lever with forelimbs and using the lever for behavioral support were dependent of the body–environment relationship.

Table A1
Analysis of the competing hypotheses based on the bi-exponential model.

Hypothesis	k	AICc	ΔAICc
1. None	3	12560.92	99.66
2. q	8	12517.19	55.94
3. b	8	12532.11	70.86
4. w	8	12528.91	67.66
5. q and b	13	12493.92	32.67
6. q and w	13	12497.93	36.68
7. b and w	13	12486.68	25.43
8. q, b and w	18	12461.25	0.00

Each hypothesis is labeled according to the parameter that was predicted to change with lever height. k is the number of free parameters in each hypothesis (parameters that are constant across heights + parameters that may vary across heights × 6 heights).

Acknowledgments

Appendix A.

We considered the likelihood that variations in parameter estimates across conditions were due to changes in the parameters of the process that generated the data, and the likelihood that these changes were due to sampling variance. Parameters w, b, and q were estimated allowing each to either vary freely across lever-height conditions, or to remain constant across conditions. This yielded $2^3 = 8$ combinations of possible constraints (e.g., q varies freely, but not w and b; q and w varies freely, but not b, etc.), each constituting a hypothesis of what parameters vary across conditions. The competing hypotheses were evaluated using the Akaike Information Criterion corrected for small samples (ΔAICc; Burnham and Anderson, 2002; Wagenmakers and Farrel, 2004). ΔAICc indicates how unlikely each hypothesis is relative to the most likely hypothesis, after correcting for the difference in the number of free parameters. More precisely, a hypothesis is $e^{\Delta AICc/2}$ times less likely than the most likely hypothesis (for which ΔAICc = 0).

ΔAICc is indicated for each hypothesis in Table A1. This criterion strongly favored the hypothesis that w, b, and q varied across lever-height conditions. The second most likely hypothesis was that q was constant across lever-height conditions, but it was $e^{12.715} \approx 332,700$ times less likely than the selected hypothesis, even after taking into consideration the difference in the number of free parameters.

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