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Object play in adult domestic cats: the roles of habituation and disinhibition

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Abstract

We have investigated the role of habituation and disinhibition in the control of object (predatory) play by adult domestic cats *Felis silvestris catus* both with and without prior experience of hunting. We hypothesised that object play is terminated by rapid habituation to the sensory characteristics of the object played with, and therefore should be disinhibited if the sensory characteristics of the object are changed. Three sequential sessions of play with an unchanging object (a toy) caused almost complete habituation of the play response; replacing the toy with one of contrasting colours in a fourth session elicited intense disinhibited play, suggesting that motivation for play itself had not diminished substantially during the first three sessions. The time interval between sessions affected the extent of disinhibition. After a long delay (25–45 min) between each session play was less intense in the fourth session than in the first; if the interval was 5 min, it was more intense, indicative of post-inhibitory rebound, possibly caused by initial positive feedback of play on its own performance. We suggest that object play by adult cats is controlled by two mechanisms derived from predatory behaviour: one responds to prey-like stimulus characteristics, such as texture and small size, which elicit play, while the second detects change in the toy. The behavioural default towards any object is initial interest if it possesses relevant stimulus characteristics, followed by rapid habituation unless these stimulus characteristics change.

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1. Introduction

Play between cat and owner, usually focussed on an object, is an important element of their relationship (Mertens and Schär, 1988), but the internal control and motivation of object play by adult cats (hereafter referred to simply as play), are not clearly understood, despite extensive speculation (Biben, 1979; Leyhausen, 1979; West, 1979; Smith, 1982). This is probably because studies of play have usually focussed upon explanations of its evolution and function, rather than proximate causes and mechanisms. Play shares many of the features of exploratory behaviour (Hinde, 1970); for example, it is investigative and has no obvious endpoint. In the absence of any external consequences, there must presumably be internal control mechanisms which stop play; for example, (1) internally-driven changes which stop play, such as dwindling play motivation, (2) other incompatible behaviour patterns which out-compete play patterns as their motivation increases relative to that of play (Fraser and Duncan, 1998), (3) consummatory behaviour patterns within play which cause play to stop when they have been performed for a predetermined duration or number of repetitions.

The external stimuli that elicit object play in adult cats are known to be those which generally have characteristics of typical prey items, such as small size, rapid movement, and a complex, furry texture (Leyhausen, 1979; Hall, 1995). There are also motivational links between hunger and object play in both juvenile (Martin and Bateson, 1985; Bateson et al., 1990) and adult cats (Hall and Bradshaw, 1998). Elucidation of the factors which influence the performance of object play may also help to shed light on those likely to control predatory behaviour.

We have explored possible mechanisms controlling play by focusing on the effects of habituation, since cats usually rapidly cease playing with individual toys (Hall, 1995), suggesting that habituation is of prime importance to the control of play performance. We hypothesise that habituation to the sensory characteristics of toys progressively inhibits the performance of play, while motivation to play with other appropriate objects in general remains unaffected. We test this by recording the decline in intensity of play as the same object is presented repeatedly, predicting that when the object is changed, play should increase in intensity compared to the preceding session. We also investigate the effects of the time interval between play sessions on the extent to which play recovers. Three experiments have been conducted, the first to establish the effects of colour and sensory contrast on habituation and disinhibition of play, the second to examine the effects of the interval between play sessions on the magnitude of disinhibition, and the third to replicate part of the second experiment on a population of cats with experience of hunting.

2. Methods

2.1. Subjects and housing

The first two experiments, 1 and 2, were conducted on 13 cats (4 males and 9 females, all neutered, aged 5–8 years), group-housed with 13 other neutered cats in two rooms (total 65 m²), connected by a corridor to an outside yard (96 m²). Indoor rooms were maintained between 19–22 °C and 40–50% humidity. All rooms contained shelves, beds and toys, and

all cats received daily grooming, play and social interaction from their caretakers. They were supplied daily at 16:00 h with a variety of commercially available brands of nutritionally complete cat food, both canned and dry. None had any hunting experience, apart from occasional insects and spiders. Experiment 3 was conducted on eight cross-bred pet cats (five males, three females, all neutered; aged 13 months to 7 years). All were reported by their owners to have been observed hunting regularly.

2.2. *Experimental treatments*

The toys used in play sessions were ellipsoidal (7.5 cm × 6.0 cm × 2.5 cm), fake-fur covered, either plain white or plain black, but otherwise identical. The covering material was never substantially damaged by the cats. Each cat was tested with a different pair of toys, to eliminate contamination from unfamiliar scent. Because play inevitably involved physical contact with the toy, and therefore potentially contamination by saliva and other scents, the toy was not changed between repeated presentations of the same colour, to ensure as far as possible that the cat recognised it as the same object with which it had been playing in the preceding session. The new toys, presented in the fourth session, would therefore have contrasted both visually, and presumably olfactorially, with that presented in the third session.

The group-housed cats were tested individually in a walled cubicle (1.4 m × 1.6 m), equipped with closed-circuit video recording. Subjects were selected because they were known to be playful and did not exhibit any fearful or other abnormal behaviour when temporarily separated from the other cats. All subjects were thoroughly familiarised with playing in the cubicle before sessions were recorded. Eight of these cats were used in Experiment 1, and three of these and five others were used in Experiment 2. The pet cats were tested in a room of their owner's house, with no other animal or person (apart from the experimenter) present; observations were dictated on to audio tape as the cat played, since it was impractical to install video equipment for each test.

The toys were offered to the cats attached to a 1 m length of string, with which the experimenter (SLH) swung the toy in a standard arc ($\pm 45^\circ$ from vertical) back and forth in front of the cat, in order to elicit play. As soon as the cat had made contact with the toy movement was stopped and the string allowed to go slack, until the cat released the toy again. Each test consisted of four 2 min sessions, starting at the first swing of the toy: during the intervals between sessions the cat was left in the area where the play had taken place, with no small object suitable for play available (although the pet cats used in Experiment 3 could not be prevented from playing with household objects, for example, furniture). Treatments were defined by the colour of the toy used in the first three sessions (always the same) and in the fourth, which was the same as in the first three sessions in the control sessions in Experiments 1 and 3, and different in the other treatments in Experiments 1 and 3, and in all treatments in Experiment 2. Testing always began at 09:30 h, to control for diurnal effects, and at least 1 day was left between test days, which preliminary experiments had indicated would minimise any effect of one treatment affecting the play response to the next. Within each experiment, each cat was presented with all treatments (three plus control in Experiment 1, three in Experiment 2, and one plus control in Experiment 3). The order in which treatments were presented to individual cats was determined according to a randomised Latin Square, in which letters were assigned at

random to treatments, rows to cats in groups of two or three, and columns to the days of the experiment. A gap of 3 weeks was left between Experiments 1 and 2 to minimise any carry-over in the three cats used in both experiments.

2.3. Behaviour recorded

The frequencies of all behaviour patterns (for ethogram see Hall and Bradshaw, 1998) recorded during the first, third and fourth experimental sessions were transcribed as they occurred from video playback or audio tape playback on to computer using the Observer system (v.3.0, Noldus Information Technology b.v). Analysis was confined to two patterns, which had been shown to indicate intermediate and high play motivation respectively in previous studies (Hall, 1995; Hall and Bradshaw, 1998); Clutch (cat holds the toy close to the body with one or both front paws), and Killbite (cat delivers a forceful bite to the toy).

2.4. Statistical analysis

We used SPSS (v. 10) to conduct repeated-measures ANOVAs on the square-root transformed frequencies of Clutch and Killbite, to estimate the effect of the independent variables within experiments (contrast between sessions 3 and 4 versus no contrast; time interval between presentations) and within treatments (between sessions).

3. Results

3.1. Experiment 1: habituation and disinhibition of play, and colour preferences

We first tested for habituation to both white and black toys, in case the cats' behaviour was affected by a colour preference. The cats received four treatments; white for three sessions, followed by black; its control treatment of white for all four sessions; the black toy for three sessions, changing to the white toy in the fourth session, and its control treatment of four sessions with the black toy. Subjects were eight cats from the cattery: the interval between each play session was 25 min. The frequency of performance of both play patterns dropped significantly from session 1 to 3, as the cats became habituated to the toy (Fig. 1a; Table 1). There was no significant effect of colour contrast (i.e. black to white versus white to black, $F_{1,7} = 1.52$, NS), and a substantial increase in frequency of play patterns when the toy was changed to the opposite colour (Fig. 1a; Table 1). This disinhibition was not complete, however, since the frequency of play patterns was significantly lower in session 4 compared to session 1 (Fig. 1a; Table 1). When the toy was not changed, the large majority of the cats did not play at all in the final session (comparing sessions 3 and 4, all $F_{1,7} < 3$, NS).

3.2. Experiment 2: effect of interval between sessions

Using eight cats from the cattery, three of which had also been subjects in the first experiment, we repeated the habituation/disinhibition procedure with three different

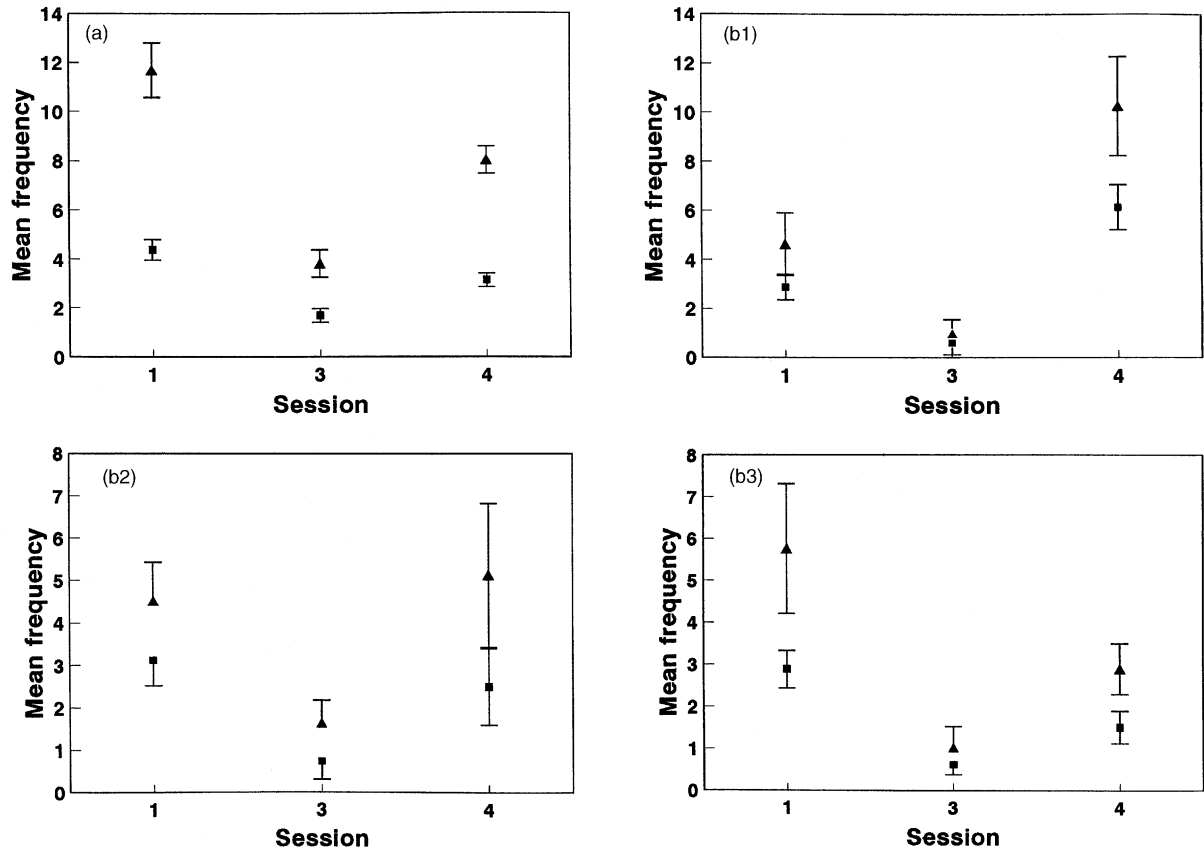


Fig. 1. Means and standard errors for frequencies of Clutch (squares) and Killbite (triangles) in sessions 1, 3 and 4 of each test where the toy was changed from white to black, or vice versa, between sessions 3 and 4. (a) Experiment 1, cattery, 25 min intervals between sessions. (b1) Experiment 2, cattery, 5 min intervals. (b2) Experiment 2, cattery, 15 min intervals. (b3) Experiment 2, cattery, 45 min intervals. (c) Experiment 3, pet cats, 5 min intervals. Overlapping error bars have been omitted for clarity.

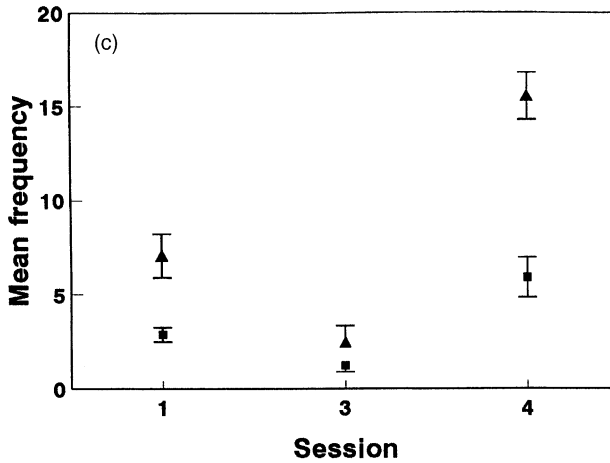


Fig. 1. (Continued).

inter-session intervals; 5, 15 and 45 min. Since the first experiment had shown no effect of colour, the sequence of three sessions with a white toy followed by one with a black toy was used throughout. As before, performance of play declined from session 1 to 3, and increased in session 4, irrespective of interval time (Fig. 1b; Table 1). However, the degree of disinhibition was affected by inter-session interval. In an ANOVA comparing sessions 1 and 4 as one main effect and all three intervals as the other, the session by interval interaction was significant for both Clutch ($F_{2,14} = 5.53$, $P < 0.02$) and Killbite ($F_{2,14} = 4.68$, $P < 0.05$). With a 45 min interval the frequency of Clutch was significantly lower in session 4 than in session 1 (Fig. 1b3). In the 15 min interval treatment, there was very little difference in the level of play between sessions 1 and 4 (Fig. 1b2). After intervals of 5 min, play performance was greater in session 4 than it had been initially (Fig. 1b1).

Table 1

The F -ratios (d.f. = 1, 7) and P -values from repeated-measures ANOVAs, in tests in which the colour of the toy was changed between sessions 3 and 4

Contrast	Pattern	Experiment 1 (25 min interval)	Experiment 2			Experiment 3: pet cats
			5 min interval	15 min interval	45 min interval	5 min interval
Session 1	Clutch	15.9, 0.02	9.00, 0.02	13.6, 0.008	21.0, 0.003	5.20, 0.06
With session 3	Killbite	14.7, 0.006	9.21, 0.02	8.75, 0.02	18.7, 0.003	7.99, 0.03
Session 3	Clutch	6.78, 0.04	56.5, <0.001	10.4, 0.02	3.94, 0.09	26.6, 0.001
With session 4	Killbite	11.1, 0.01	17.0, 0.004	6.24, 0.04	7.00, 0.03	29.9, 0.001
Session 1	Clutch	11.5, 0.01	8.05, 0.03	0.39, 0.55	5.61, 0.05	7.98, 0.026
With session 4	Killbite	12.1, 0.01	9.14, 0.02	0.22, 0.65	2.33, 0.17	17.1, 0.004

3.3. Experiment 3: disinhibition in cats with experience of hunting

To confirm that the rebound in play in session 4 with the 5 min interval was not a peculiarity of the group-housed cats, the procedure with 5 min delays was repeated on pet cats with experience of hunting, to determine whether the lack of predatory experience among the cattery cats had affected their motivation to play. Play declined from session 1 to 3, indicating habituation (Fig. 1c) and then rebounded in session 4 in the treatment in which the toy was changed, to a higher level than initially (Table 1). When the toy was not changed, only one cat played in the fourth session. Apart from a higher overall performance of Killbite in the pet cats, this result is essentially similar to that obtained from the cattery cats when the same interval was used. When the data from sessions 1 and 4 with a 5 min interval from both pet and cattery cats was combined, nested repeated-measures ANOVA indicated similar levels of play overall comparing the pet cats with the cattery cats (Clutch $F_{1,14} = 0.09$, $P = 0.77$; Killbite $F_{1,14} = 2.5$, $P = 0.13$), and no interaction between session and type of cat (Clutch $F_{1,14} = 0.08$, $P = 0.79$; Killbite $F_{1,14} = 0.67$, $P = 0.43$). The intense disinhibition observed is therefore likely to be general to all cats, rather than an abnormal behaviour induced by lack of opportunity for predation in a specific cattery.

4. Discussion

Both pet and cattery cats habituated to the unchanging toy, as indicated by the decline in the intensity of play by the third session. When a new toy, which contrasted with that used in the third session both in colour and presumably in odour, was presented in the fourth session the play response was disinhibited. The intensity of the disinhibited play in the fourth session was affected by the length of the delay between sessions. When the delay was long (25–45 min) play did not regain its initial intensity. However, with less time between sessions, the intensity of the disinhibited play response was higher; it was roughly equal to its initial level when the delay was 15 min, and was actually higher than in the first session when the delay was short (5 min). Such an increase, in which the disinhibited response is more intense than it was initially, is qualitatively distinct from the simple recovery in which the disinhibited play is no more intense than it was initially. It has been termed post-inhibitory rebound (Kennedy, 1985; Nicol, 1987), and has been proposed as an indicator of frustration and hence diminished welfare when observed in farm animals (Nicol, 1987; Petherick and Rushen, 1997).

It therefore appears that object play by adult cats is exploratory, with a system of habituation and feedback from play performance controlling its expression and determining when it stops. Habituation to an unchanging toy causes cats to stop playing, although the length of time for this to occur depends upon the sensory value of the toy (Hall, 1995), which was kept constant in the present experiments. That disinhibited play can return to its initial intensity, or higher (depending on the circumstances) indicates that play motivation remains high and does not diminish despite inhibition of play by habituation to an unchanging toy.

The effect of the duration of the interval between play sessions can also be explained in terms of motivation. The post-inhibitory rebound when the interval is short suggests that

the performance of play may be governed by an initial positive feedback (McFarland, 1993), i.e. motivation to play is increasing at the same time as its performance is being suppressed by habituation to the unchanging toy, and if the total duration of the play test is short, a marked rebound in play performance occurs when the toy is changed and expression of play is disinhibited. The effects of this feedback presumably dissipate when the delay time between sessions is longer (15 min or more). This leads to the expression of play which, though disinhibited, is reduced in intensity compared to its initial level. It is also possible that during the long delay between play sessions, the motivation to perform other types of behaviour begins to take precedence over the motivation to play.

Thus, the overall control system for play behaviour appears to have at least two components. The behavioural default is to habituate rapidly to a toy after initial interest and play. Unless there is a change in the toy stimuli, play, which has been inhibited, will not be performed again. A change in the toy stimuli enables play to be expressed again. The second aspect of the control of play is the influence of the sensory value of the toy, which modifies the effect of habituation and disinhibition on play performance (Hall, 1995).

The origins of this system may be explained by comparison of object play by adult cats with predation, to which it is structurally similar and also probably motivationally very similar (Hall and Bradshaw, 1998). In predatory behaviour, any object (including prey) which possesses particular stimulus characteristics associated with prey, such as small size and furry texture, receive attention and can elicit play as well as predation (Rasa, 1973; Leyhausen, 1979; Russell, 1990). Rapid habituation could prevent unnecessary performance of predatory behaviour with unsuitable or inanimate objects, or those which do not change despite contact from the cat's teeth and/or claws. This control involves two mechanisms, which may be explained in terms of innate releasing mechanisms (IRM; Tinbergen, 1951). Of the two controlling object play, and therefore probably predation, the first is an excitatory IRM, which is sensitive to particular object characteristics and sensory quality, is modifiable by experience, and both initiates and sustains play (Biben, 1979). Possession of any of these qualities by an object stalls the habituation process, enabling further predatory behaviour/play. The second, inhibitory, IRM operates only once play has begun, and is sensitive to the object's 'changeability': the cat habituates rapidly to a prey animal which does not change as predation progresses (i.e. is neither physically damaged, nor becomes contaminated with the cat's saliva). In actual predation, lack of change in a prey animal may be because it is strong or large enough to resist the cat's predatory attempts. Despite possessing the qualities to which the first IRM is sensitive, habituation occurs. However, if the prey animal changes, that is, becomes physically damaged, or a new prey item appears (our protocol mimics both of these eventualities), the cat will not habituate and therefore will continue with predatory behaviour.

The timing of the post-inhibitory rebound can also be explained by homologies with hunting behaviour. Free-ranging domestic cats hunt in bouts of about 30 min (Turner and Meister, 1988), which is consistent with our observation that initial positive feedback from (predatory) play stimuli lasts for about 15–30 min.

We conclude that object play by adult cats is usually terminated by habituation to the sensory characteristics of the object. Motivation to play can remain high, however, since if a new object is encountered within a few minutes of play having been terminated by

habituation, it resumes at high intensity. These observations are consistent with the hypothesis that object play by adult cats is homologous with predatory behaviour.

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