Department of Psychology, Birkbeck College

Course PSYC044U (Psychobiology II.) WEEK **3**
February 8 2007

HABITUATION AND PAVLOVIAN CONDITIONING

Lecture on Habituation, sensitization and stimulus learning

Topic

Habituation is measured as the decline in an already-present response to the repetition of a single stimulus.

- The methodology for habituation experiments is very straightforward — a single stimulus is repeatedly presented, and the strength of an initally present response is measured.
- Sometimes the repitition of a single stimulus leads to increases in responsiveness to it — the phenomena is called "**Sensitization**".
- More often, with stimuli which are not very strong or which have little motivational significance, repitition leads to a decline in any response to them. This waning of responsiveness is known as "habituation".
- Habituation can be regarded as a "global principle of adaptation" (Davey, 1989) since it can be observed in a very wide range of species.
- It is possible to obtain the basic result in relatively simple neural systems (e.g. *Aplysia*, the mammalian spinal cord) and it is therefore necessary to distinguish habituation as a form of learning from forms of sensory and response fatigue.
- Even when this can be done habituation in simple neural systems is clearly likely to be explicable in terms of basic neuronal processes and the properties of individual neurons (e.g. Carew and Kandel, 1973; Castellucci and Kandel, 1976; Bristol and Carew, 2005; Shafer, 2005;Hawkins et al., 2006).
- However, the methodology of habituation can also be applied to perception in normal human subjects, and is particularly useful in studies of perceptual development in human preverbal infants (Sokolov, 1963; Maurer and Maurer, 1988, Olson, 1976, Kellman and Spelke, 1983, Csibra, 2003; Phillips & Wellman, 2005; O'Connell and Dunbar, 2005; Temple et al., 2006).
- In these cases explanations of the phenomena of habituation may involve more complex processes relating to stimulus categorization and representation, and interactions with the attentional and motivational processes which are associated with the dimension of stimulus novelty and familiarity.
- (See also the notes on habituation later on in the handout at pages 4 – 7).

Sample essay

To what extent should habituation be regarded as a simple form of learning?

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NOTES ON HABITUATION

Habituation as discussed by Humphrey in *The Nature of Learning* (1933)

A shadow thrown on sea urchin makes it raise its spines; but if the stimulus is repeated 3 or 4 times visible reaction ceases. This has been called 'aclimatisation', 'accommodation, or 'negative adaptation' and is an example of characteristic biological equilibrium.

Habituation is ubiquitous: it is found in amoeba and other single-celled animals; hyrda, sea anemones worms, parasitic grubs, barnacles, larva of mosquitos bivalve molluscs, snails. (water snails under trees moving in wind ignore shadows, but the same species where no trees very reactive.) many vertebrates and insects; (cows on railway embankments; humans living in cities don't notice traffic noise.)

BUT NOT ALL SPECIES USE THE SAME mechanism — apparent habituation can be found in species with no nervous system. It can be in receptor systems, or 'central'.

An Experiment (Humphrey, 1933 p 136)

Land snails on an oak platform 18x5in - on ball bearings. Electrically produced jerks given at regular intervals, usually 2 secs. The response measured was withdrawing into the shell. There were individual differences. After habituation one snail did not react to the blow of hammer on the board, and some would be half on the board and half on the table, and still not react when the board was jerked. If these snails were given half-min rests then the response re-appeared, but with repeated half-min rests there is longer term habituation. The phenomena cannot be attributed to fatigue since a *new stimulus* e.g. a steel ball dropped on the board, will produce the response.

Comments

Habituation is distinguishable from response *fatigue* in a physiological sense in this instance, but not always, especially if no nervous system.

Thompson and Spencer (1966) Used hindlimb flexion reflex of the acute spinal cat, and list 9 characteristics of habituation they found.

1. Repeated stimulation ⇒ decreased response.
2. Then no stimulation ⇒ **spontaneous recovery** over time. (? how long)
3. If 1. & 2. repeated ⇒ habituation becomes quicker (long term Habituation)
4. More frequent stimulation ⇒ more rapid habituation
5. Weaker stimulation ⇒ more rapid or stronger Habituation
6. Further stimulation after Habituation ⇒ delayed recovery of response.
7. Habituation generalizes to similar stimuli.
8. A separate stimulus ⇒ response recovery (=**dishabituation**).
9. If 8. repeated ⇒ dishabituation disappears.

Pinsker *et al* (1970)
Used the sea-slug *Aplysia*: gill withdrawal reflex in response to a jet of seawater — this habituated over 10 trials at 3-min intervals.

Results - 6 of the above 9 characteristics were found; missing 3, 6 & 7. (with shorter inter-trial intervals, 3. can sometime be observed - Castellucci and Kandel, 1976)

The Mechanism in *Aplysia* is that sensory pre-synaptic terminals release progressively less neurotransmitter, and this produces decrements in the excitatory post-synaptic potentials (EPSPs). When there is dishabituation, this is because activity of the sensory pre-synaptic terminals is facilitated. (Castellucci and Kandel, 1976; Kandel, 2001).

Sokolov (1975: see Gray, 1976, p.6 and Walker, 1987, p.39-41, or Green 1987, chapter 7)

Sokolov studied *adult human Ss*. Uses the term "extinction of the orienting reflex" to refer to habituation. The orienting reflex is not modality specific (up to a point) but a generalised response to novelty. It is measured by —

1. Increased sensory sensitivity (and attention?)
2. Drop in skin resistance (GSR)
3. Reduced alpha rhythms in the EEG
4. Constriction of peripheral blood vessels.
5. Cephalic vasodilation (opposite to 4. in the head.
6. Lowering of respiration and pulse rates.

These things *don't happen* to an habituated stimulus.

Human *Ss* show the "missing stimulus effect": there is dishabituation if a stimulus is absent in a normally regular sequence. This shows some kind of pre-attentive extrapolation from previous experience. Habituation in human subjects is related to attention and memory.

Habituation in Pre-Verbal Human Infants

For visual stimuli direction of gaze can be monitored by independent observers or video cameras
For auditory stimuli, measures such as heart-rate deceleration or general movement can be taken. (see Gleitman, Fridlund and Reisberg, 1999, p. 554 or Gleitman 1995, p. 512-3)

Cornell (1974)
Ss 5-month olds shown photos of faces, 6 times, 110-s each time. They lose interest over 6 trials but are aroused when a different face is first used.

Bundy *et al* (1982)
Ss= 4 months sensitive to changes in simple melodies but only when fundamental and first three harmonics present.

Kellman & Spelke (1983)
224 3-4 mo olds were habituated to 1 object whose top and bottom were visible but whose center was occluded by a nearer object. They were then tested with a fully visible continuous object and with 2 fully visible object pieces with a gap where the occluder had been. Patterns of dishabituation suggested that infants perceived the boundaries of a partly hidden object by analyzing the movements of its surfaces: Infants perceived a connected object when its ends moved in a common translation behind the occluder. (Gleitman et al., 1999; pp. 554)

Csibra, G. (2001). 8 month olds perceive illusory contour (Kanizsa) figures as occluding surfaces.

Csibra, G. (2003) 9 and 12 month olds perceive moving dots as agents trying to achieve goals.

Results of exposure to a stimulus

(as in Walker 1987 p. 37 ff)

i) Sensory adaptation or fatigue

But Dethier (1963) showed that blowfly adaptation to certain sugar solution transferred from left to right leg- therefore more central In fact generalized sensory adaptation could be marginal form of habituation.

ii. Response fatigue

Response decline would be less interesting if due just to muscular exhaustion. But **dishabituation** with a second stimulus shows that it is not just a response-production process

iii. Habituation in the S-R connection:

"Habituation involves homosynaptic depression of the [presynaptic] terminal due to repeated activity of the sensory neurons" (Castellucci and Kandel, 1976). There are decrements in excitatory post-synaptic potentials of the motor cell, because pre-synaptic terminals of sensory cell release less transmitter substance. Thus it is the central synapses between sensory input and motor output that habituate.

iv. Sensitization and Sensitized states

Often there is opposite of habituation which is like "warm-up": "Sensitization means that the early stages of repeated exposure to a stimulus are characterised by increases in the strength of the responses made to the stimulus. Groves and Thompson have separated habituating synapses and sensitized circuits, even in spinal cords. (Groves & Thompson 1970: see overhead on sheet **8**). Kandel's Nobel lecture included a section on results obtained using sensitization as a test of memory processes (Kandel, 2001).

v. Familiarity by memory formation of the stimulus.

(Sokolov overhead on sheet **9**)

Sometimes called "extinction of the orienting reflex" which is confusing, but refers to changes in attention peripherally very observable in infants. Alternatively "Formation of a neuronal model of the stimulus"

vi.. Decreased attention to familiar stimuli (Sokolov, sheet 5)

Attention can be indicated by desynchronisation of EEG and eye turning. Plus dilation of blood vessels in the head and drop in resistance of skin of hands ("GSR").Thus gating of incoming stimuli, which must involve multi-stage hierarchically organized perceptual systems. This *cannot* happen in the same way with spinal or ganglionic reflexes. even though some ecological **functions** are similar.

vii. Increased capacities for discrimination and classification.

By exposure, increased perceptual accuracy (Hebb, 1949) .Gibson and Walk (1956): rats reared in cages with bas-reliefs of circles and triangles on the walls were better at experimental discrimination. Thus "Perceptual learning" exposure learning or "latent learning". The main function of perception is not to become indifferent but to acquire useful information. The ecological function of habituation is more widespread with complex perceptual systems. In more complex systems the ecological function is stimulus recognition. (**Imprinting** is an example of this.)

Few people deny that Habituation occurs in humans

Schicatano, E. J., & Blumenthal, T. D. (1994). Caffeine delays habituation of the human acoustic startle reflex. *Psychobiology, 22*(2), 117-122.

The acoustic startle reflex has proved to be an excellent system for studying habituation in mammals. In animal studies, startle habituation has been found to be sensitive to various pharmacological manipulations. The present experiments were designed to determine whether caffeine (4 mg/kg) modified startle habituation in low and high caffeine users. Human eyeblink responses were measured in a startle habituation paradigm in which 30 trials of 85-dB broadband noise stimuli with a duration of 50 msec and a rise time of .1 msec were presented. Caffeine delayed the habituation of startle amplitude in both low and high users and produced significant dishabituation in low users. These findings indicate that caffeine disrupts early sensory filtering.

— or jellyfish

Johnson, M. C., & Wuensch, K. L. (1994). An investigation of habituation in the jellyfish *Aurelia aurita*. *Behavioral and Neural Biology, 61*(1), 54-59.

Three experiments were conducted to examine the effectiveness of different forms of tactile stimulation, probe and stream, and interstimulus intervals (ISI) in producing habituation in the polypoid sessile stage of the jellyfish Aurelia aurita. Results from Experiment 1 showed that polyps significantly decreased their responsiveness to both forms of tactile stimulation with 30- s ISI across 60 trials. Response to a novel stimulus indicated that the response decrement had not been due to fatigue. When the ISI was lengthened to 6 min in Experiment 2, response to the probe form of tactile stimulation did not significantly decrease across 20 trials. Using an ISI of 1 min in Experiment 3, response to the probe form of tactile stimulation decreased significantly across 40 trials. A significant increase in response to the original stimulus (**dishabituation**) following presentation of a novel stimulus indicated that response decrement was due to habituation or a habituation- like process rather than simple effector fatigue or sensory adaptation.

Caenorhabditis elegans

See Habituation refs Broster and Rankin (1994), Wicks and Rankin (1996) and Staddon & Higa (1996)

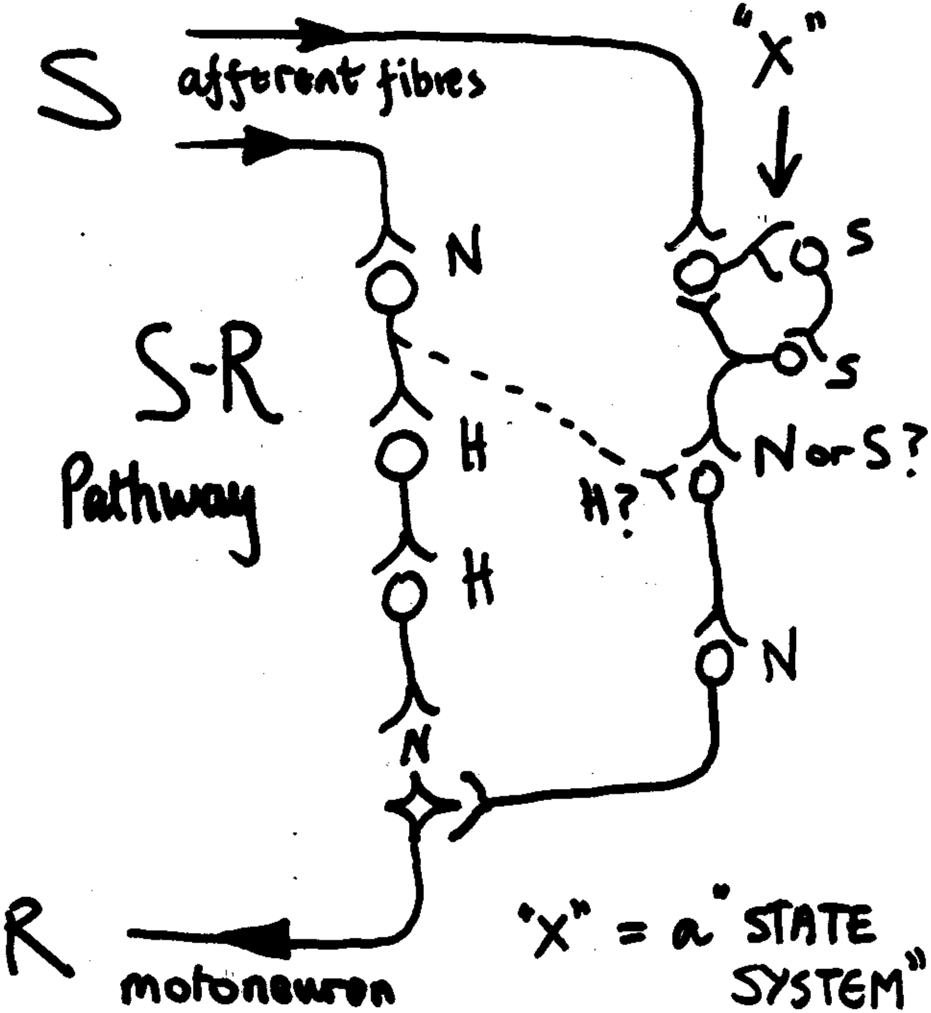
Many biologists work on this species because it is a simple animal. The exact sequence of all its DNA was completed in 1998 (Hodgkin, Jasny, B.R. and Kimble, J. (*Science*, Dec 11th, 1998)

It is a thread worm, only 1 mm long that lives in soil.

Its body is made up of 959 cells, of which 81 are muscle cells and 302 are neurons

Although habituation of its “reverse-swimming” response varies according to the Inter-Stimulus-Interval (ISI) the data can be modelled by “a remarkably simple process” (Staddon and Higa, 1996), which corresponds to two habituating neurons in the S-R (stimulus-response) pathway (cf Groves and Thompson, 1970)

GROVES + THOMPSON (1970)



3 types of synapse

① NON-PLASTIC (N)

② DECREMENTAL, HABITUATING (H)

③ INCREMENTAL, SENSITIZING, (S)

from Walker (1987)

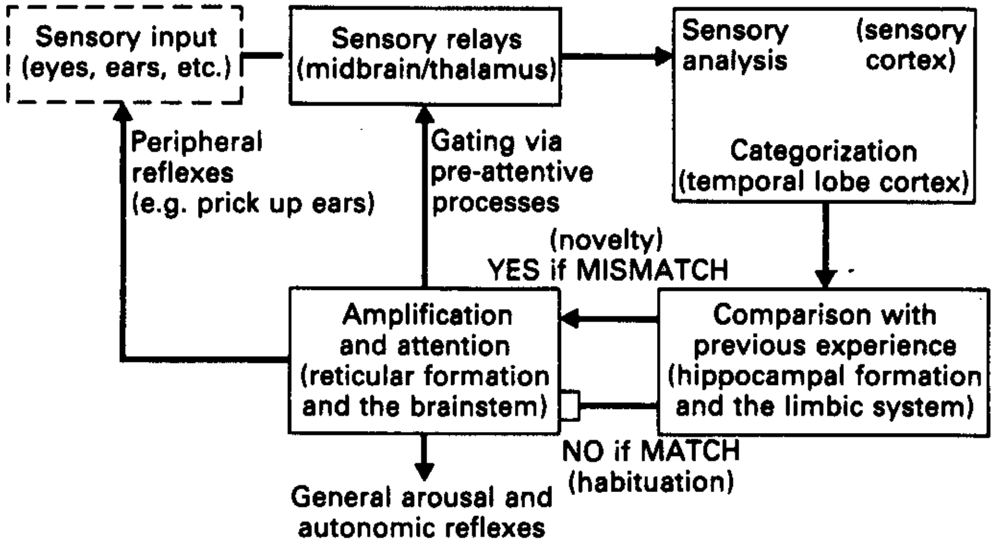
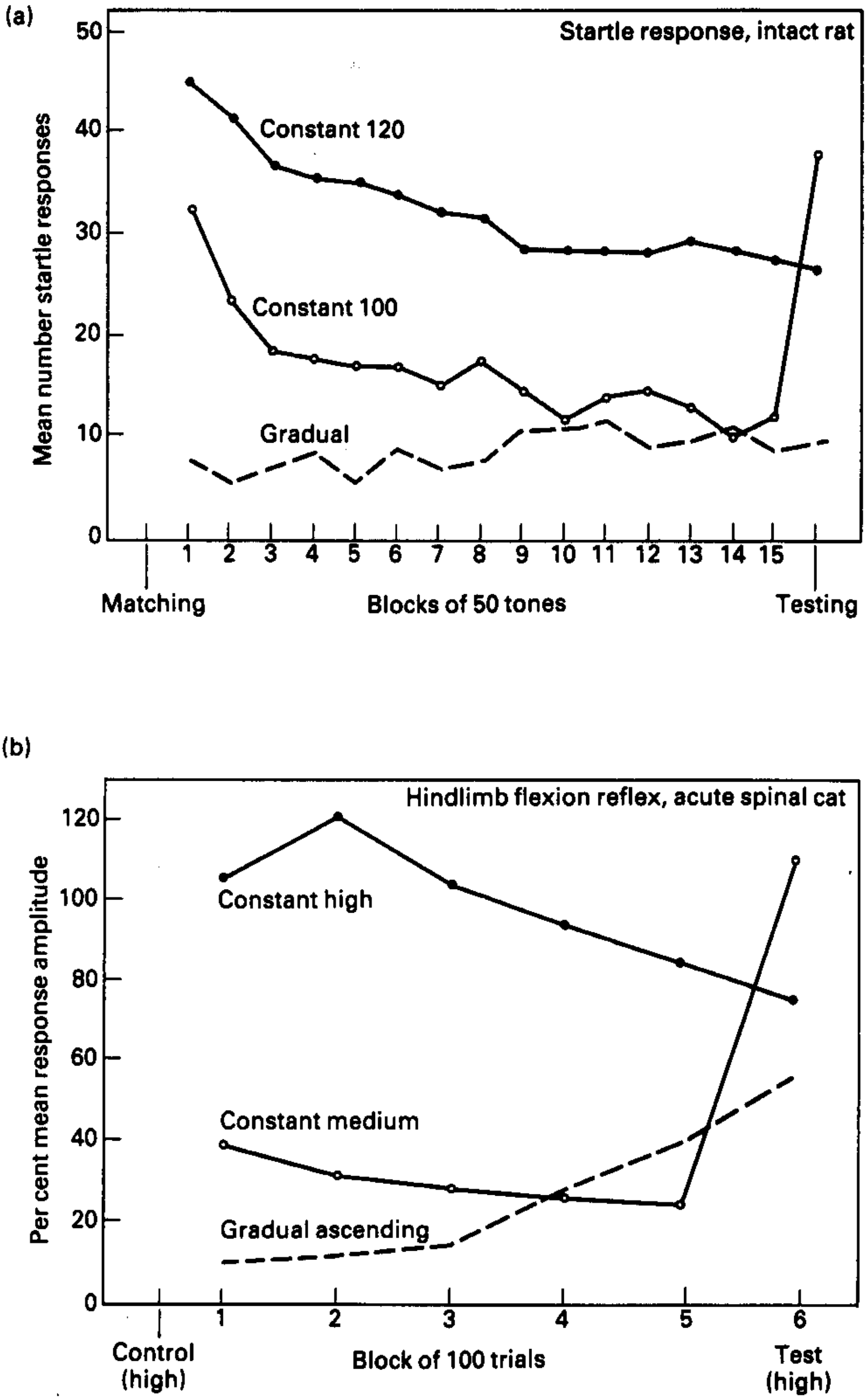


Figure 2.1 *Sokolov's theory of habituation.* After Sokolov (1963, 1975).

there is a match between the two, the incoming stimulus can be ignored.

(vi) Decreased attention to familiar stimuli

Given a comparator mechanism, any response orginally given to a stimulus, such as the drawing-in of a snail's horns, may be suspended when the stimulus has become familiar and matches expectations. However, in Sokolov's theory, emphasis is given to physiological reactions, measurable in human subjects, which are correlated to some degree with the attention and arousal generated by incoming stimuli. Such responses are selected partly for convenience, and partly because they appear to be useful indicators of stimulus novelty. They include, understandably, the turning of the head and eyes towards the source of a localized stimulus, and the desynchronization of the electroencephalograph (EEG) which is known to occur with subjective attention to external stimuli in normal human adults. Slightly less obviously, responses which are in practice correlated with stimulus novelty include dilation of blood vessels in the head, and the from Walter (1987)



10

Lecture 2: Pavlovian (Classical) Conditioning

Topic

The most basic procedure of Pavlovian conditioning is the pairing of two stimuli, with the expected outcome being that responses originally only elicited by one of them will be also elicited by the other. Usually the conditioned stimulus (CS), which only elicits the response after training, can be said to operate as a signal for the other (the Unconditioned Stimulus,— US or UCS). Important variations on the simplest procedure include Discrimination, where one stimulus (CS+) is paired with the UCS, and another (CS-) is not.

In Pavlov's experiments dogs salivated to signals for food, but classical conditioning is studied in many other contexts.

Theoretical questions include the nature of the associations responsible for conditioning, and the critical conditions for producing associations.

WHAT IS ASSOCIATED?

The main possibilities are associations between the conditioned stimulus and the measured unconditioned response, and associations between the two stimuli. The general conclusion is that it is ***associations between the stimuli*** which are important, the main theory being that of **stimulus-substitution.**

WHAT CAUSES THE ASSOCIATION?

The obvious first assumption would be that associations are caused by the stimulus-pairings, that is by ***contiguity***. This principle is sometimes known as the "Hebb rule" after Hebb (1949) who proposed that this operated at the level of associations between neurons. However, at the behavioural level the contiguity explanation is rejected in favour of ***contingency***: it can be shown that the strength of an association between two stimuli depends on the ***conditional probability*** of their conjunction, rather than on the absolute number of pairings (Rescorla, 1967, 1988). Thus "conditioning is now described as the learning of relations among events." (Rescorla, 1988; see also Pearce & Bouton, 2001).

There are two other empirical findings which argue against the exclusive importance of stimulus pairings.

(i) Blocking (Kamin, 1969). Loosely, it appears that if animals are already expecting food, then a new signal which is paired with it is not noticed: "A useful shorthand is that organisms adjust their Pavlovian associations only when they are 'surprised'." (Rescorla, 1988, p.153; Lieberman, 2000, Chap 3, pp 107-115).

(ii) Qualitative relations between stimuli. Stimuli may become associated even though they are ***never*** paired. This can happen in "Taste-aversion learning" (Garcia and Koelling, 1966; Garcia, 1981; Lieberman, 2000 pp 82-83 and pp. 115-119) or the "cue to consequence effect": animals appear to associate the taste of something they have eaten previously with becoming ill some time later. Similarity between stimuli is an additional variable when they are paired. (Rescorla, 1988; p. 154)

WHAT IS SUBSTITUTED FOR WHAT?

Classical conditioning phenomena are observed in a wide variety of contexts (Bouton et al., 2001; Cardinal et al., 2002; Lorenzetti et al., 2006; Mineka and Ohman, 2002; Qi et al., 2006; Stockhurst et al., 2006) which are likely to differ greatly in the involvement of motivational systems and in the level of perceptual representation of the stimuli. Exactly what gets associated with what depends on the context, and in particular on the stimuli used (see Walker, 1987; pp. 100-4 and 65-91).

Sample Essay.

To what extent is classical conditioning explicable in terms of the principle of contiguity (stimulus pairings)?

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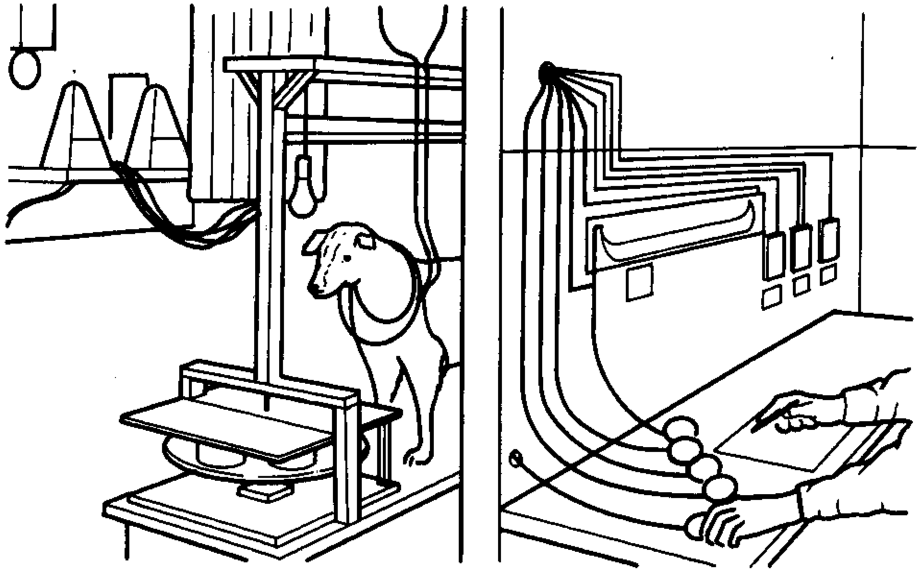


Figure 3.1 *Pavlov's method.*
Pavlov's experiments were very carefully controlled. The dog was isolated from the experimenter, who delivered stimuli by means of automated devices, and recorded quantitative measures of response. After Asratyan (1953).

of his research, he discovered that psychological factors had such powerful effects:

> generally speaking, the outstanding role of psychological stimulation in the processing of food in the digestive canal has not met with proper acknowledgement. Our investigations forced us to bring these influences to the fore. Appetite, the craving for food, is a constant and powerful stimulus to the gastric glands. There is not a dog in which skilful teasing with food does not evoke a more or less considerable secretion of juice in the empty and hitherto inactive stomach. (1955, p. 141)

In order to study psychological effects on digestive secretions more thoroughly, it was enough to measure the effects of selected artificial stimuli on volume of salivation, and this could be accomplished by means of a minor operation to lead salivation out through a tube in the dog's cheek. The experimental methods adopted in Pavlov's laboratories were very systematic: the dog was usually separated from the

Procedures and phenomena in Classical (Pavlovian) Conditioning

a) Acquisition

b) Extinction

c) Spontaneous Recovery

d) Discrimination

e) Conditioned Inhibition

Pavlov's more cognitive view

"So infinitely complex, so continuously in flux, are the conditions of the world around, that the complex animal system which is itself in living flux, and that system only, has a chance to establish **a dynamic equilibrium with the environment.** Thus we see that the most general function of the hemispheres is that of reacting to signals presented by innumerable stimuli of interchangeable signification" (Pavlov 1927 chap 1)

More recent cognitive views

Mackintosh (1983, p22) says animals detect "a true causal relation between the events to be associated"

Gray (1979) says Classical Conditioning enables the animal ***to learn the relationship between stimulus events in its world*** (p64).

See also Rescorla (1988) *"Pavlovian conditioning: It's not what you think it is"*

Kamin (1969) "Predicability, surprise, attention and conditioning"

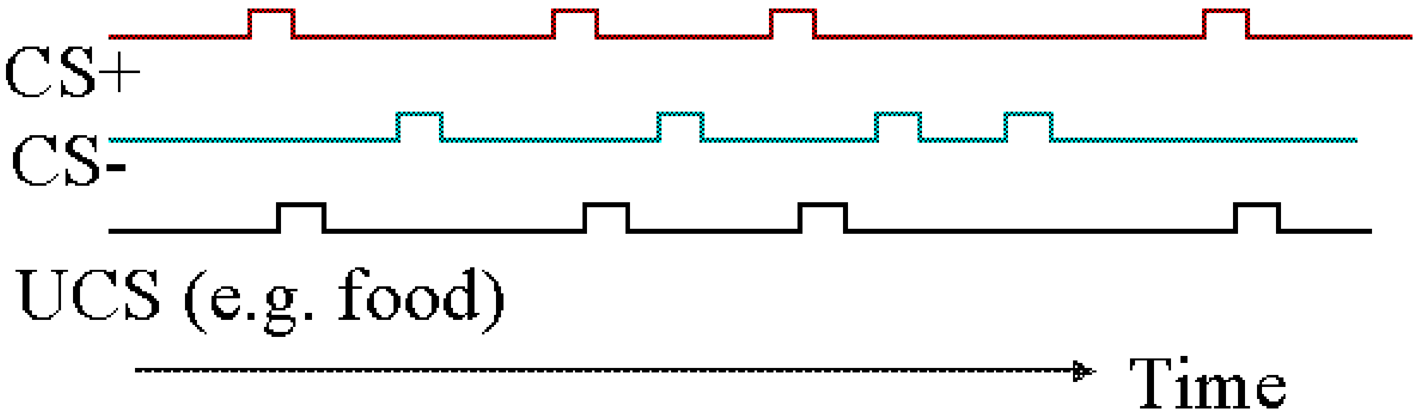
An experiment on "blocking"

Conditioned stimuli could be:

L = a light
N = a noise

or both together (L+N)

Group	1st stage (no of sessions)	2nd stage of training	TEST	Result: Effect of L alone
A	L+N (8)	N(16)	L	50%
B	N (16)	L+N (8)	L	10%
C		L+N (8)	L	90%
D		N (24)	L	8%



There are two conditioned stimuli.

One is positive (CS+) and occurs just before the unconditioned stimulus (UCS: e.g. food).

The other stimulus is negative (CS—), and is not followed by the US (the abbreviations US and UCS are used interchangeably.

[page 16 of paper handout]

Pavlovian conditioning is interpreted as the formation of an association between two stimuli.

Usually the "unconditioned stimulus" (US or UCS) reliably elicits a response before the experiment (this is known as the unconditioned response: UCR or UR) and the association is measured by the degree to a new event (the "conditioned stimulus" or CS) comes to elicit the same response during the course of the experiment.

The simplest rule to explain association formation is that the association is increased whenever the conditioned stimulus precedes and overlaps with the unconditioned stimulus — the rule of **contiguity**.

The simple rule of contiguity is inadequate: current theories relate strength of association to the **predictive properties of a signalling stimulus** (Rescorla, 1988; Lieberman, 2000).

Three experimental results support this —

Phenomena showing that stimulus-pairing (contiguity) is not the only factor in Pavlovian conditioning.

1. Contingency. If a bell is paired with food 10 times during one hour, the contiguity rule would imply that the bell should elicited conditioned responses (e.g. salivation). But if, during the same hour, food has also been given 20 times without the bell, or the bell has sounded 20 times without being followed by food, then the bell will not be a reliable predictor of food, and experiments suggest that the strength of conditioned responses usually varies according to the reliability of the conditioned stimulus as a predictor of the unconditioned stimulus.

2. Blocking. Even if a signal predicts food reliably, there is little conditioning effect if it is redundant, because an alternative reliable signal has already been used. E.g. if a light has been the signal for food 100 times and then the light plus a sound is used as a compound signal 100 times, testing with the bell alone shows little conditioning (but it does if the initial trials with the light are omitted.

3. Relevance of the stimulus. The main experimental phenomenon here is **taste-aversion learning**: animals (and people) readily associate tastes of particular foods with illness, even if the taste has been experienced hours before the illness (i.e. there is no contiguity: Garcia and Koehling, 1966).

This leads to a more cognitive "information processing view" of conditioning in animals than the "knee-jerk" idea of conditioned reflexes. However when classical conditioned associations occur in people they are distinctive in being involuntary, and not verbally accessible (e.g. Brewin, 1989).

Ss. 10 rats in each of 4 groups, tested in small box with a drinking spout, in which every lick of the spout could be counted.

Procedure

1 week of habituation to drinking plain water in the box.

Pre-tests "bright-noisy" water (flashing light and clicks when the spout was licked) and "tasty" water (with flavours added).

Training: e.g with lithium. One 20-min session every 3 days in which rats could drink only water with added lithium chloride (which they cannot distinguish from salty water), with the "bright-noisy" stimuli also present. These were interpolated with days when the rats were tested with plain water – no extra stimuli. And since no lithium, no aversive effects.

A group was run for which the floor was briefly electrified 2 sec after licks at the spout, (with test and trials 2 min long. on NRRN, RNNR, per day, 4 days.

and a group where similar shocks were delayed for longer, to produce a decline in drinking of the same kinds as that seen in the lithium group, run on same schedule as the lithium group.

Testing. Subgroups of *Ss* with water accompanied by just the audio-visual cue, and water with just the flavour cue – 2 days after last reinforced trial.

Results

Ss trained with gastric distress (either due to lithium, or X-irradiation) subsequently suppressed drinking of the flavoured water much more than the water accompanied by audio-visual cues used in training.

Conversely the rats which had received peripheral aversive stimulation in training suppressed drinking in the presence of the audio-visual cue, but not with the flavour cue.

SIMILARITIES AND DIFFERENCES BETWEEN HABITUATION AND CLASSICAL CONDITIONING (See Walker, 1987, Ch. 4 esp pp 114-6)

1. Differences include

1.1 Procedural differences – Habituation involves repeated presentation of the same single stimulus whereas classical conditioning involves the pairing of or predictive relationships between two stimuli.

1.2 Behavioural outcomes – the effect of habituation is the decline in a previously present response, whereas in classical conditioning the main effect is the shifting of a previously available response to a new stimulus.

1.3 Explanatory mechanisms. Classical conditioning is usual interpreted in terms of the formation of associations between stimuli, whereas habituation is explained by the decline in **response** to a stimulus, or as a result of more complex processes of stimulus recognition.

1.4 Although habituation is a very basic mechanism, few deny that it occurs in human subjects, whereas classical conditioning in human subjects is often said to involve cognitive process (see week 4)

2. Similarities include

2.1 Levels of representation. The basic phenomena of both habituation and classical conditioning are found in biological systems of vastly different internal complexity and mode of operation. They are very widespread across species.

2.2 Behavioural functions. Theories of how associative processes operate in classical conditioning cluster around the detection of a discrepancy between expected and observed events (Rescorla and Wagner, 1972). Similarly, theories of habituation can be described in terms of the formation of an accurate internal model of external experience (Sokolov, 1963, 1975). Both processes serve to adapt simple behaviours to the details of recent experience, and can be regarded as reducing environmental unpredictability (cf. Davey, 1989, p.199 paragraph 2), even though the mechanisms utilized to accomplish this may vary in complexity.