

LECTURE 1: REWARD AND PUNISHMENT IN INSTRUMENTAL LEARNING (OPERANT CONDITIONING)

Topic

Instrumental conditioning differs, at least at first sight, from Pavlovian conditioning in that i) new response patterns emerge and ii) responses are “goal-directed”. An early experimental and theoretical analysis of instrumental learning was given by **Thorndike** (1898, 1901: reprinted 1998) who studied cats escaping from “problem boxes” in which it was necessary for them to pull a loop of string, press a lever (or make some other artificial response) in order to get out. Thorndike explained the results by the “Law of Effect” which supposes that the positive motivational consequences of behaviours influence learning, but only by “stamping-in” connections between successful responses and the circumstances in which they were performed. Thus, although goal achievement affects learning, the resulting behaviours are not goal directed in the sense of being modified by any kind of internal anticipation of their outcomes. Mechanisms of this kind undoubtedly exist in many species, including mammals (Brembs 2003; Eisenstein & Carlson, 1994; Packard and Knowlton, 2002; Segal and Wolf, 1994; Hawkins et al., 2006). An even more reductionist “stimulus-response” theory of instrumental learning was put forward by Hull (1943, 1952), and elaborate procedures for controlling the outcome of instrumental procedures were devised by Skinner (1938; Ferster and Skinner, 1957) without further elaboration of Thorndike’s “Law of Effect” explanation.

A more cognitive interpretation of instrumental learning phenomena is due to **Tolman** (1932, 1948), and this is broadly supported by subsequent analyses (Dickinson, 1985; Mackintosh, 1983; Rescorla, 1991; Lieberman, 2000; Brown & Giumetti, 2006; Raby et al., 2006). Tolman’s view was that the animals in his experiments made use of “cognitive maps” of the environment and its significant features, and formed “expectancies” with regard to specific goals. Two main kinds of experimental evidence can be used to argue against the Thorndikean “Law of Effect” and in favour of more purposive theories.

1. *Spatial Learning.* Most of Tolman’s own experiments were on maze learning, where results such as the use of novel short-cuts, and the apparent utilization of spatial knowledge for differing modes of locomotion (swimming round mazes previous learned when dry: Macfarlane, 1930) are difficult to explain in terms of stimulus-response habits. The term “cognitive map” has its critics, because the evidence suggests that the representation of spatial relationships in insects (Giufra and Capaldi, 1999; Wehner et al., 2006), rats (Hogarth et al., 2000) and indeed humans (Wang and Spelke, 2000; Foo et al., 2005) is not as rich as the term “cognitive map” would suggest. However, Tolman’s basic points, that there are internal representations of space of some kind, and internal representations of rewards, as opposed to blind habits alone, are no longer in dispute (Jacobs, 2003; Jacobs and Schenck, 2003; Menzel et al., 2005). Although this supports a cognitive interpretation of the effects of incentives, much current work on “reward-circuits” emphasises that these circuits are facilitated by the effects of addictive drugs. All addictive drugs have in common that they enhance (some directly, some indirectly) dopaminergic function at crucial dopamine pleasure/reward synapses in the *nucleus accumbens*. (Berridge, 1996; Cardinal and Everitt, 2004; Everitt & Robbins, 2005; Davis et al., 2004; Ikemoto and Panksepp, 1999; Rodd et al., 2004; Vanderschuren & Everitt 2004; Hyman et al., 2006; Wise, 2006).

2. *Reward re-evaluation.* In Tolmanian accounts of instrumental learning, responses are produced as means to ends (and are thus “actions” rather than “habits”). Such accounts can be tested by direct alternations of the reward-value of goals. Early experiments on “latent learning” (Tolman and Honzik, 1930) demonstrated that in a familiar maze rats will return immediately to a location in which they have once previously found food. In the “radial maze” (Olton and Samuelson, 1976) rats appear to use a working memory of places where they have already finished all available food on a given day. Extensive work on the devaluation of specific rewards for specific responses also suggests that there are associative links between learned responses and their customary outcomes (Crespi, 1942 – see page 11; Dickinson, 1985; Rescorla, 1991; Percearo et al., 1999; Cowill and Triola, 2002, Colwill, 2006; Yin et al., 2004; Corbit and Balleine, 2005; Balleine, 2005; Wang et al., 2005).

Sample Essay

To what extent was Thorndike correct in assuming that instrumental learning can be fully accounted for by the strengthening of connections between preceding stimuli and successful responses?

LECTURE 2: COMPARISONS OF CLASSICAL AND INSTRUMENTAL CONDITIONING

“Classical conditioning can be regarded as a rather primitive, automatic consequence of certain associations: instrumental conditioning requires that the organism utilize the information embodied in certain associations in order to reach certain conclusions.”

Mackintosh (1983), p. 112

“It seems likely that there are at least two kinds of human long-term learning, one of which is open to conscious reflection (perhaps based on instrumental conditioning), and influenced by the capacity to verbalise a strategy, while the other is implicit and independent of verbalization (perhaps based on Pavlovian conditioning?)”

Baddeley (1990) p. 206.

Topics

Although there have been attempts to explain both Pavlovian and Instrumental conditioning in terms of a single underlying associative principle, there are a number of behavioural and physiological features which suggest differentiation between Pavlovian and instrumental learning (see the table attached). For instance, instrumental procedures appear not to be directly effective in modifying the responsiveness of the autonomic nervous system (Dworkin and Miller, 1986) while Pavlovian procedures are not suitable for producing substantial changes in repertoires of motor skills. A critical theoretical distinction is that Pavlovian conditioning is **not** sensitive to motivational pay-offs, whereas instrumental learning, by definition, **is**.

An experimental test derived from this is the use of an ‘*omission*’ procedure to check if supposedly Pavlovian responses are sensitive to changes in pay-offs (e.g. Sheffield, 1965; Williams and Williams, 1969: see Lieberman, 2000 pp. 443-444; or 1993, pp.345-346). Neuroscientific evidence tends to support separate brain mechanisms for classical and instrumental conditioning (Dickenson et al., 2000; Ikemoto and Pankseep, 1999; Leszczuk and Flaherty, 2000; Balleine, 2005; Baldwin et al., 2002; Baxter & Byrne, 2006; Shultz, 2006; Spicer et al., 2007 — informally ‘reward-seeking’ can be different from ‘reward-anticipation’ and ‘wanting’ can be different from ‘liking’ – Berridge and Robinson, 2003; Wilson et al., 2006).

However, many natural behaviours and laboratory tests are likely to be influenced by **both** Pavlovian and instrumental processes. A particular instance is the procedure of “*autoshaping*” in pigeons, in which the species-specific response of pecking can be used in stimulus-pairing procedures, where it is resistant to loss of pay-offs (Williams and Williams, 1969), but at the same time can be shown to be highly sensitive to instrumental contingencies in other contexts (Ferster and Skinner, 1957; Lieberman, 1993, pp. 215-225 or 2000, pp. 220-229).

Apart from comparisons between Pavlovian and instrumental learning conceived of as learning processes which can apply very generally across species, and across behaviours in any species, a second question is the degree to which any kind of learning is either species- or domain-specific: that is, how far it should be regarded as a specialized solution to a particular biological problem, as opposed to a generally applicable principle. An important test case is “taste-aversion learning” (Garcia and Koelling, 1966; Garcia, 1981; already discussed in Weeks 3 and 4), which at first sight appears to be a good candidate for a highly specialized learning process. It is however very general across species, and it is arguable that it is a specialized form of classical conditioning, rather than a different learning process altogether (Revusky, 1985; Garcia *et al*, 1977; Davey, 1989). Similarly, in many species instrumental learning as studied in the laboratory can be viewed as an adaptation to aid optimal foraging for food (Lea, 1979, 1984; Baum et al. 1999). The *assessment of experienced pay-offs*, suggested above as one of the defining features of instrumental learning, would clearly be important in many kinds of foraging, but may have even more general applicability (Brembs, 2003; Kringelback & Rolls, 2004; Lorenzetti et al., 2006; Baxter & Byrne, 2006; Lea & Webley, 2006).

Sample essay

Compare and contrast classical and instrumental conditioning.

Main Sources

Lieberman, D. (1993/2000) *Learning: Behavior and Cognition*. Belmont: Wadsworth. (in 1993: pp 57-65, 166-185, 215-231, 325-9 & 343-356/ in 2000: pp. 41-2, 163-167, 192-234 & 442-449).

Walker, S.F. (1985) *Animal Thought*. Routledge & Kegan Paul: London. (pp. 61-94).

Walker, S.F. (1987) *Animal Learning: An Introduction*. Routledge & Kegan Paul: London. (CHAPTER 5, ‘Instrumental Learning’ and Chapter 6 ‘Biological bases of classical and instrumental conditioning’, pp. 165-202.)

There is also basic material on these topics to be found in the Gleitman et al texts, as follows:

Page reference in Gleitman et al 2004	Page reference in Gleitman et al 1999	Page reference in Gleitman 1995	Textbook Heading
132-3	128-9	115-6	“Instrumental Learning”
143, 147	140, 144	126, 143	“Cognitive Learning/Cognitive Maps”
118	111	99-100	“The Biology of Reward”

Further Reading

- Davey, G. (1989) *Ecological Learning Theory*. London: Routledge. CHAPTER 3. and (Ch 6, “The Biological Function of Classical Conditioning” and pp 225-254 for optimal foraging)
- Carlson, N. (1998) *Physiology of Behavior. 6th edn* Allyn & Bacon: Needham Heights. pp. “Reinforcement”, pp 441-449; “Common features of addiction”, pp565-584. (6 copies, 3-1wk & 3-3wk loan in BK library)
- Baddeley, A.D. (1990) *Human Memory*. Hove, Lea: Chapter 9, “Acquiring Habits”, pp. 201-232.

Other References (not normally needed for further reading)

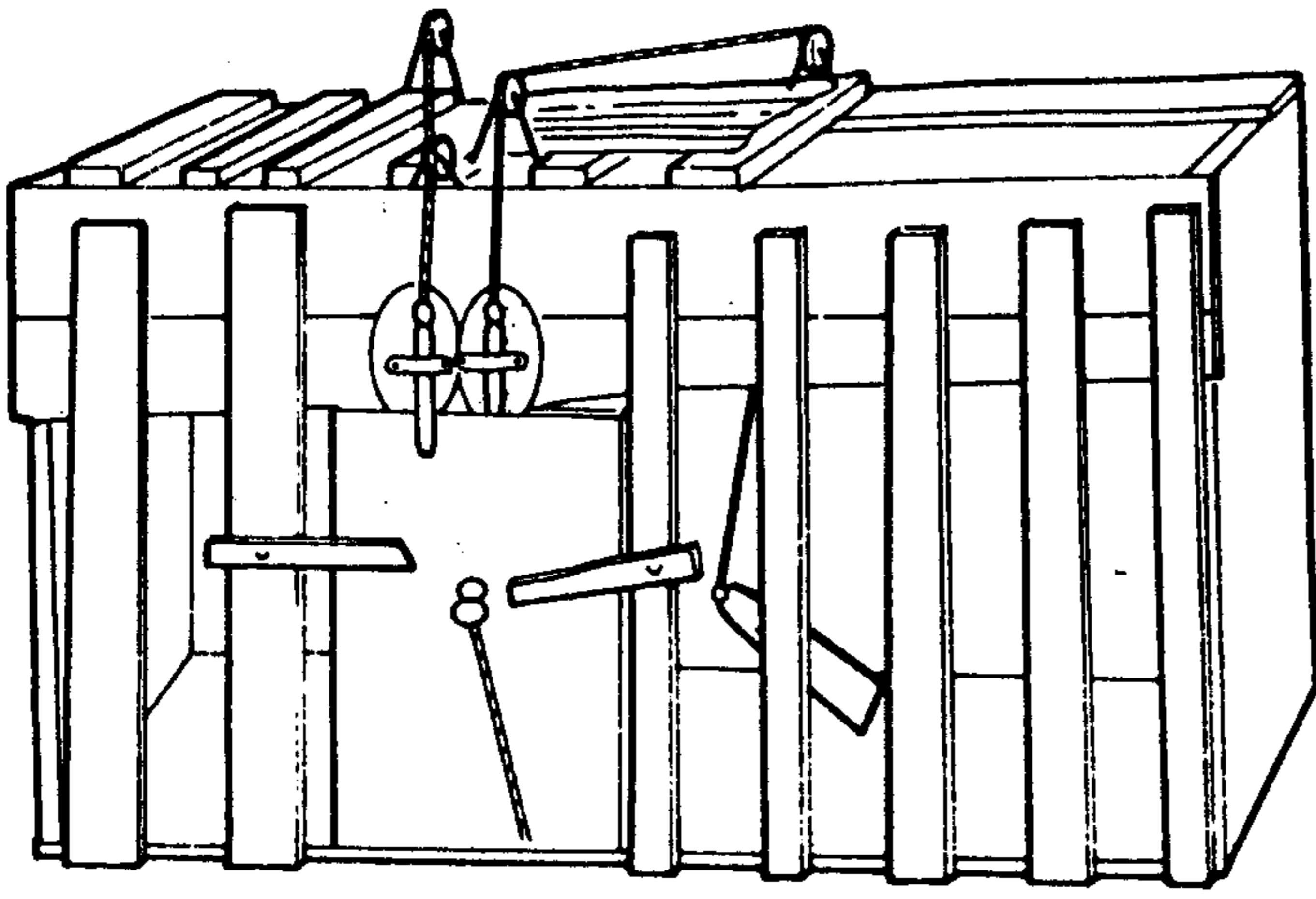
- Adams, C.D. (1982) Variations in the sensitivity of instrumental responding to reinforcer devaluation. *Quarterly Journal of Experimental Psychology*, 34B, 77-98.
- Amiez, C., Joseph, J. P., & Procyk, E. (2006). Reward encoding in the monkey anterior cingulate cortex. *Cerebral Cortex*, 16(7), 1040-1055.
- Anderson, K. G., & Woolverton, W. L. (2000). Concurrent variable-interval drug self-administration and the generalized matching law: A drug-class comparison. *Behavioural Pharmacology*, 11(5), 413-420.
- Aron, A., Fisher, H., Mashek, D. J., Strong, G., Li, H. F., & Brown, L. L. (2005). Reward, motivation, and emotion systems associated with early-stage intense romantic love. *Journal of Neurophysiology*, 94(1), 327-337.
- Atallah, H. E., Lopez-Paniagua, D., Rudy, J. W., & O'Reilly, R. C. (2007). Separate neural substrates for skill learning and performance in the ventral and dorsal striatum. *Nature Neuroscience*, 10(1), 126-131.
- Baldwin, A. E., Sadeghian, K., Holahan, M. R., & Kelley, A. E. (2002). Appetitive instrumental learning is impaired by inhibition of cAMP-dependent protein kinase within the nucleus accumbens. *Neurobiology of Learning and Memory*, 77(1), 44-62.
- Balleine, B. W. (2005). Neural bases of food-seeking: Affect, arousal and reward in corticostriatolimbic circuits. *Physiology & Behavior*, 86(5), 717-730.
- Balleine, B. W., Killcross, A. S., & Dickinson, A. (2003). The effect of lesions of the basolateral amygdala on instrumental conditioning. *Journal of Neuroscience*, 23(2), 666-675.
- Balleine, BW and Dickinson, A (1998) The role of incentive learning in instrumental outcome revaluation by sensory-specific satiety. *Animal Learning & Behavior*, Vol.26, No.1, Pp.46-59.
- Bartels, A., & Zeki, S. (2004). The neural correlates of maternal and romantic love. *Neuroimage*, 21(3), 1155-1166.
- Bateson, M & Kacelnik, A (1995) Accuracy of memory for amount in the foraging starling, *Sturnus-vulgaris*. *Animal Behaviour*, Vol.50, No.Pt2, Pp.431-443.
- Baum, W. M., & Kraft, J. R. (1998). Group choice: Competition, travel, and the ideal free distribution. *Journal of the Experimental Analysis of Behavior*, 69(3), 227-245.
- Baum, W. M., Schwendiman, J. W., & Bell, K. E. (1999). Choice, contingency discrimination, and foraging theory. *Journal of the Experimental Analysis of Behavior*, 71(3), 355-373.
- Baxter, D. A., & Byrne, J. H. (2006). Feeding behavior of *Aplysia*: A model system for comparing cellular mechanisms of classical and operant conditioning. *Learning & Memory*, 13(6), 669-680.
- Belke, T. W. (2000). Studies of wheel-running reinforcement: Parameters of Herrnstein's (1970) response-strength equation vary with schedule order. *Journal of the Experimental Analysis of Behavior*, 73(3), 319-331.
- Berridge, K. C. (1996). Food reward: Brain substrates of wanting and liking. *Neuroscience and Biobehavioral Reviews*, 20(1), 1-25.
- Berridge, K. C., & Robinson, T. E. (1998). What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Research Reviews*, 28(3), 309-369.
- Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences*, 26(9), 507-513.
- Blaisdell, A. P., & Cook, R. G. (2005). Integration of spatial maps in pigeons. *Animal Cognition*, 8(1), 7-16.
- Blundell, P., Hall, G., & Killcross, S. (2001). Lesions of the basolateral amygdala disrupt selective aspects of reinforcer representation in rats. *Journal of Neuroscience*, 21(22), 9018-9026.
- Braida, D., Pozzi, M., Cavallini, R., & Sala, M. (2002). 3,4-methylenedioxymethamphetamine (ecstasy) impairs eight-arm radial maze performance and arm entry pattern in rats. *Behavioral Neuroscience*, 116(2), 298-304.
- Breland, K. and Breland, M. (1961) The misbehaviour of organisms. *American Psychologist*, 16, 681-4.
- Brembs, B. (2003). Operant conditioning in invertebrates. *Current Opinion in Neurobiology*, 13(6), 710-717.
- Brembs, J., Lorenzetti, F. D., Reyes, F. D., Baxter, D. A., & Byrne, J. H. (2002). Operant reward learning in *Aplysia*: Neuronal correlates and mechanisms. *Science*, 296(5573), 1706-1709.
- Brown, M. F., & Giumetti, G. W. (2006). Spatial pattern learning in the radial arm maze. *Learning & Behavior*, 34(1), 102-108.

- Brown, P.L. and Jenkins, H.M. (1968) Autoshaping of the pigeon's key peck. *Journal of the Experimental Analysis of Behaviour*, 11, 1-8.
- Caldwell, A. B. (2001). What do the MMPI scales fundamentally measure? Some hypotheses. *Journal of Personality Assessment*, 76(1), 1-17.
- Cardinal, R. N., & Everitt, B. J. (2004). Neural and psychological mechanisms underlying appetitive learning: links to drug addiction. *Current Opinion in Neurobiology*, 14(2), 156-162.
- Colwill, R. M. (2006). Passage of time leaves response-outcome associations intact. *Behavioural Processes*, 72(1), 91-99.
- Colwill, R. M., & Triola, S. M. (2002). Instrumental responding remains under the control of the consequent outcome after extended training. *Behavioural Processes*, 57(1), 51-64.
- Colwill, R.M. and Rescorla, R.A. (1985) Post-conditioning devaluation of a reinforcer affects instrumental responding. *Journal of Experimental Psychology: Animal Behaviour Processes*, 11, 120-132.
- Colwill, R.M. and Rescorla, R.A. (1990) Effect of reinforcer devaluation on discriminative control of instrumental behaviour. *Journal of Experimental Psychology: Animal Behaviour Processes*, 16, 40-47.
- Corbit, L. H., & Balleine, B. W. (2003). The role of prelimbic cortex in instrumental conditioning. *Behavioural Brain Research*, 146(1-2), 145-157.
- Corbit, L. H., & Balleine, B. W. (2005). Double dissociation of basolateral and central amygdala lesions on the general and outcome-specific forms of pavlovian-instrumental transfer. *Journal of Neuroscience*, 25(4), 962-970.
- Corbit, L. H., Muir, J. L., & Balleine, B. W. (2001). The role of the nucleus accumbens in instrumental conditioning: Evidence of a functional dissociation between accumbens core and shell. *Journal of Neuroscience*, 21(9), 3251-3260.
- Crespi, L.P. (1942) Quantitative variation in incentive and performance in the white rat. *American Journal of Psychology*, 55, 467-517.
- Davis, C., Strachan, S., & Berkson, M. (2004). Sensitivity to reward: implications for overeating and overweight. *Appetite*, 42(2), 131-138.
- Di Ciano, P., & Everitt, B. J. (2004). Conditioned reinforcing properties of stimuli paired with self-administered cocaine, heroin or sucrose: implications for the persistence of addictive behaviour. *Neuropharmacology*, 47, 202-213.
- de Wit, S., Niry, D., Wariyar, R., Aitken, M. R. F., & Dickinson, A. (2007). Stimulus-outcome interactions during instrumental discrimination learning by rats and humans. *Journal of Experimental Psychology-Animal Behavior Processes*, 33(1), 1-11.
- Dickinson, A (1985) Actions and habits: the development of behavioural autonomy. *Proceedings of the Royal Society, B*, 308, 67-78.
- Dickinson, A., Smith, J., & Mirenowicz, J. (2000). Dissociation of Pavlovian and instrumental incentive learning under dopamine antagonists. *Behavioral Neuroscience*, 114(3), 468-483.
- Dragoi, V., & Staddon, J. E. R. (1999). The dynamics of operant conditioning. *Psychological Review*, 106(1), 20-61.
- Dworkin, B, and Miller, N.E. (1986) Failure to replicate visceral learning in the acute curarized rat preparation. *Behavioural Neuroscience*, 100, 299-314.
- Eisenstein, EM, Carlson, AD. (1994) Leg position learning in the cockroach nerve cord using an analog technique. *Physiology & Behavior*, Vol.56, No.4, Pp.687-691.
- Everitt, B. J., & Robbins, T. W. (2005). Neural systems of reinforcement for drug addiction: from actions to habits to compulsion. *Nature Neuroscience*, 8(11), 1481-1489.
- Everitt, B. J., Dickinson, A., & Robbins, T. W. (2001). The neuropsychological basis of addictive behaviour. *Brain Research Reviews*, 36(2-3), 129-138.
- Ferster, C.B. and Skinner, B.F. (1957) *Schedules of Reinforcement*. Appleton-Century-Crofts: New York.
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *J. Exp. Psy. -Learning Memory and Cognition*, 31(2), 195-215.
- Gallistel, C.R. (1990) *The Organization of Learning*. Cambridge, Mass.: MIT Press
- Garcia, J. (1981) Tilting at the paper mills of academe. *American Psychologist*, 36, 149-58.
- Garcia, J., Ervin, F., Yorke, C. and Koelling, R. (1967) Conditioning with delayed vitamin injections. *Science*, 155, 716-8.
- Garcia, J., Hankins, W. and Rusiniak, K. (1974) Behavioural regulation of the *milieu interne* in man and rat. *Science*, 185, 824-31.
- Gibson, B. M., & Kamil, A. C. (2001). Tests for cognitive mapping in Clark's nutcrackers (*Nucifraga columbiana*). *Journal of Comparative Psychology*, 115(4), 403-417.
- Goss-Custard, J.D. (1977) Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Animal Behaviour*, 25, 10-29.
- Harper, D.G.C. (1982) Competitive foraging in mallards: 'ideal free' ducks. *Animal Behaviour*, 30, 575-584.
- Hawkins, R. D., Clark, G. A., & Kandel, E. R. (2006). Operant conditioning of gill withdrawal in *Aplysia*. *Journal of Neuroscience*, 26(9), 2443-2448.
- Herrnstein, R.J. (1970) On the law of effect. *Journal of the Experimental Analysis of Behaviour*, 13, 243-66.
- Herrnstein, R.J. (1977) The evolution of behaviourism. *American Psychologist*, 32, 593-613.
- Hogarth, L. A., Roberts, W. A., Roberts, S., & Abrams, B. (2000). Spatial localization of a goal: Beacon homing and landmark piloting by rats on a radial maze. *Animal Learning and Behavior*, 28(1), 43-58.
- Hogarth, L., Dickinson, A., Hutton, S. B., Elbers, N., & Duka, T. (2006). Drug expectancy is necessary for stimulus control of human attention, instrumental drug-seeking behaviour and subjective pleasure. *Psychopharmacology*, 185(4), 495-504.

- Holland, P. C., & Petrovich, G. D. (2005). A neural systems analysis of the potentiation of feeding by conditioned stimuli. *Physiology & Behavior*, 86(5), 747-761.
- Hull, C.L. (1943) *Principles of Behaviour*. Appleton-Century-Crofts: New York.
- Hull, C.L. (1952) *A Behaviour System*. Yale University Press: New Haven.
- Hyman, S. E., Malenka, R. C., & Nestler, E. J. (2006). Neural mechanisms of addiction: The role of reward-related learning and memory. *Annual Review of Neuroscience*, 29, 565-598.
- Ikemoto, S., & Panksepp, J. (1999). The role of nucleus accumbens dopamine in motivated behavior: A unifying interpretation with special reference to reward-seeking. *Brain Research Reviews*, 31(1), 6-41.
- Ikemoto, S., & Wise, R. A. (2004). Mapping of chemical trigger zones for reward. *Neuropharmacology*, 47(Supplement 1), 190-201.
- Inglis, IR, Forkman, B and Lazarus, J (1997) Free food or earned food? A review and fuzzy model of contrafreeloading. *Animal Behaviour*, Vol.53, No.Pt6, Pp.1171-1191.
- Jacobs, L. F. (2003). The evolution of the cognitive map. *Brain Behavior and Evolution*, 62(2), 128-139.
- Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review*, 110(2), 285-315.
- Jenkins, H.M. and Moore, B.R. (1973) The form of the autoshaped response with food or water reinforcers. *Journal of the Experimental Analysis of Behaviour*, 20, 163-81.
- Knutson, B., Adams, C. M., Fong, G. W., & Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. *Journal of Neuroscience*, 21(16), U1-U5.
- Konorski, J. and Miller, S. (1937) On two types of conditioned reflex. *Journal of General Psychology*, 16, 264-72.
- Krebs, J.R. and Davies, N.B. (eds.) (1983) *Behavioural Ecology. An Evolutionary Approach*. 2nd Edition.. Blackwell Scientific Publications: Oxford.
- Krebs, J.R., Kacelnik, A. and Taylor, P. (1978) Tests of optimal sampling by foraging great tits. *Nature*, 275, 27-31.
- Kringelbach, M. L., & Rolls, E. T. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, 72(5), 341-372.
- Lea, S. E. G., & Webley, P. (2006). Money as tool, money as drug: The biological psychology of a strong incentive. *Behavioral and Brain Sciences*, 29(2), 161-+.
- Lea, S.E.G. (1979) Foraging and reinforcement schedules in the pigeon: optimal and non-optimal aspects of choice. *Animal Behaviour*, 27, 875-86.
- Lea, S.E.G. (1984a) *Instinct, Environment and Behaviour*. Methuen: London
- Leszczuk, M. H., & Flaherty, C. F. (2000). Lesions of nucleus accumbens reduce instrumental but not consummatory negative contrast in rats. *Behavioural Brain Research*, 116(1), 61-79.
- Lorenzetti, F. D., Mozzachiodi, R., Baxter, D. A., & Byrne, J. H. (2006). Classical and operant conditioning differentially modify the intrinsic properties of an identified neuron. *Nature Neuroscience*, 9(1), 17-19.
- MacFarlane, D.A. (1930) The role of kinaesthesia in maze learning. *University of California Publications in Psychology*, 4, 277-305.
- Mackintosh, N.J. (1983) *Conditioning and Associative Learning*. Clarendon Press: Oxford. Chapter 4, 'Theoretical analysis of instrumental conditioning, pp 77-112.
- Menzel, R., De Marco, R. J., & Greggers, U. (2006). Spatial memory, navigation and dance behaviour in *Apis mellifera*. *Journal of Comparative Physiology a-Neuroethology Sensory Neural and Behavioral Physiology*, 192(9), 889-903.
- Menzel, R., Greggers, U., Smith, A., Berger, S., Brandt, R., Brunke, S., et al. (2005). Honey bees navigate according to a map-like spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*, 102(8), 3040-3045.
- Miller, N.E. (1969) Learning of visceral and glandular responses. *Science*, 163, 434-44.
- Miller, N.E. (1978) Biofeedback and visceral learning. *Annual Review of Psychology*, 29, 373-404.
- Miller, N.E. and Dicara, L. (1967) Instrumental learning of heart-rate changes in curarized rats: shaping, and specificity to discriminative stimulus. *Journal of Comparative and Physiological Psychology*, 63, 12-19.
- Nelson, A., & Killcross, S. (2006). Amphetamine exposure enhances habit formation. *Journal of Neuroscience*, 26(14), 3805-3812.
- Neuringer, A.J. (1969) Animals respond for food in the presence of free food. *Science*, 166, 399-401.
- Olton, D.S. (1979) Mazes, maps, and memory. *American Psychologist*, 34, 583-96.
- Olton, D.S. and Samuelson, R.J. (1976) Remembrance of places passed: spatial memory in rats. *Journal of Experimental Psychology: Animal Behaviour Processes*, 2, 97-116.
- Osthaus, B., Lea, S. E. G., & Slater, A. M. (2005). Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Animal Cognition*, 8(1), 37-47.
- Packard, M. G., & Knowlton, B. J. (2002). Learning and memory functions of the basal ganglia. *Annual Review of Neuroscience*, 25, 563-593.
- Raby, C. R., Alexis, D. M., Dickinson, A., & Clayton, N. S. (2007). Planning for the future by western scrub-jays. *Nature*, 445(7130), 919-921.
- Rescorla, R.A. (1991) Associative relations in instrumental learning: The eighteenth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology*, 43B, 1-23.
- Rescorla, R.A. (1994) Control of instrumental performance by Pavlovian and instrumental stimuli. *Journal of Experimental Psychology: Animal Behaviour Processes*, 20, 44-50.
- Roberts, A. C. (2006). Primate orbitofrontal cortex and adaptive behaviour. *Trends in Cognitive Sciences*, 10(2), 83-90.

- Rodd, Z. A., Bell, R. L., Sable, H. J. K., Murphy, J. M., & McBride, W. J. (2004). Recent advances in animal models of alcohol craving and relapse. *Pharmacology Biochemistry and Behavior*, 79(3), 439-450.
- Rolls, E. T. (2004). The functions of the orbitofrontal cortex. *Brain and Cognition*, 55(1), 11-29.
- Schultz, W. (2006). Behavioral theories and the neurophysiology of reward. *Annual Review of Psychology*, 57, 87-115.
- Segal, R.L., Wolf, S.L. (1994) Operant-conditioning of spinal stretch reflexes in patients with spinal-cord injuries. *Experimental Neurology*, Vol.130, No.2, Pp.202-213.
- Seligman, M.E.P. (1970) On the generality of the laws of learning. *Psychological Review*, 77, 406-18..
- Sheffield, F.D. (1965) Relation between classical conditioning and instrumental learning. In Prokasy, W.F. (ed.) *Classical Conditioning*. Appleton-Century-Crofts: New York, 302-322.
- Shiels, K., Hawk, L. W., Richards, J. B., & Colder, C. R. (2007). Individual differences in conditioned reward: The observing procedure. *Personality and Individual Differences*, 42(1), 15-25.
- Skinner, B.F. (1938) *The Behaviour of Organisms*. Appleton-Century-Croft: New York.
- Skinner, B.F. (1977) Herrnstein and the evolution of behaviourism. *American Psychologist*, 32, 1006-12.
- Small, D. M., Zatorre, R. J., Dagher, A., Evans, A. C., & Jones-Gotman, M. (2001). Changes in brain activity related to eating chocolate - From pleasure to aversion. *Brain*, 124, 1720-1733.
- Spicer, J., Galvan, A., Hare, T. A., Voss, H., Glover, G., & Casey, B. J. (2007). Sensitivity of the nucleus accumbens to violations in expectation of reward. *Neuroimage*, 34(1), 455-461.
- Thorndike, E.L. (1898) Animal Intelligence: an experimental study of the associative processes in animals. *Psychological Review, Monograph Supplements*, 2(8), 1-109. (excerpt re-printed 1998, *American Psychologist*, 53, 1125-1127.)
- Thorndike, E.L. (1931) *Human Learning*. Century: London.
- Tindell, A. J., Smith, K. S., Pecina, S., Berridge, K. C., & Aldridge, J. W. (2006). Ventral pallidum firing codes hedonic reward: When a bad taste turns good. *Journal of Neurophysiology*, 96(5), 2399-2409.
- Tinkelpaugh, O.L. (1928) An experimental study of representative factors in monkeys. *Journal of Comparative Psychology*, 8, 197-236.
- Tolman, E.C. (1932) *Purposive Behaviour in Animals and Men*. Century: New York.
- Tolman, E.C. (1948) Cognitive maps in rats and men. *Psychological Review*, 55, 189-208.
- Tolman, E.C. (1949) There is more than one kind of learning. *Psychological Review*, 56, 144-155
- Tolman, E.C. and Honzik, C.H. (1930b) Introduction and removal of reward, and maze learning in rats. *University of California Publications in Psychology*, 4, 257-75.
- Tolman, E.C., Ritchie, B.F. and Kalish, D. (1946) Studies in spatial learning: I. Orientation and the short cut. *Journal of Experimental Psychology*, 36, 13-24.
- Vanderschuren, L., & Everitt, B. J. (2004). Drug seeking becomes compulsive after prolonged cocaine self- administration. *Science*, 305(5686), 1017-1019.
- Volkow, N. D., Fowler, J. S., & Wang, G. J. (2004). The addicted human brain viewed in the light of imaging studies: brain circuits and treatment strategies. *Neuropharmacology*, 47, 3-13.
- Wang, G. J., Volkow, N. D., Thanos, P. K., & Fowler, J. S. (2004). Similarity between obesity and drug addiction as assessed by neurofunctional imaging: A concept review. *Journal of Addictive Diseases*, 23(3), 39-53.
- Wang, R. X. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, 77(3), 215-250.
- Wang, S. H., Ostlund, S. B., Nader, K., & Balleine, B. W. (2005). Consolidation and reconsolidation of incentive learning in the amygdala. *Journal of Neuroscience*, 25(4), 830-835.
- Watanabe, M., Cromwell, H. C., Tremblay, L., Hollerman, J. R., Hikosaka, K., & Schultz, W. (2001). Behavioral reactions reflecting differential reward expectations in monkeys. *Experimental Brain Research*, 140(4), 511-518.
- Wehner, R., Boyer, M., Loertscher, F., Sommer, S., & Menzi, U. (2006). Ant navigation: One-way routes rather than maps. *Current Biology*, 16(1), 75-79.
- Williams, D.R. and Williams, H. (1969) Auto-maintenance in the pigeon: sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behaviour*, 12, 511-20.
- Wilson, D. I. G., Laidlaw, A., Butler, E., Hofmann, D., & Bowman, E. M. (2006). Development of a behavioral task measuring reward "wanting" and "liking" in rats. *Physiology & Behavior*, 87(1), 154-161.
- Wise, R. A. (2006). Role of brain dopamine in food reward and reinforcement. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 361(1471), 1149-1158.
- Yin, H. H., Knowlton, B. J., & Balleine, B. W. (2004). Lesions of dorsolateral striatum preserve outcome expectancy but disrupt habit formation in instrumental learning. *European Journal of Neuroscience*, 19(1), 181-189.

...and, eventually and by accident, make the
opened the door to the box it was confined in.
in the simplest box, Box A, there was a large w



7

Figure 5.1 *Thorndike's problem box.*
See text. After Thorndike (1898).

Liberman (2000) pp195-6.
(1993) 59-60

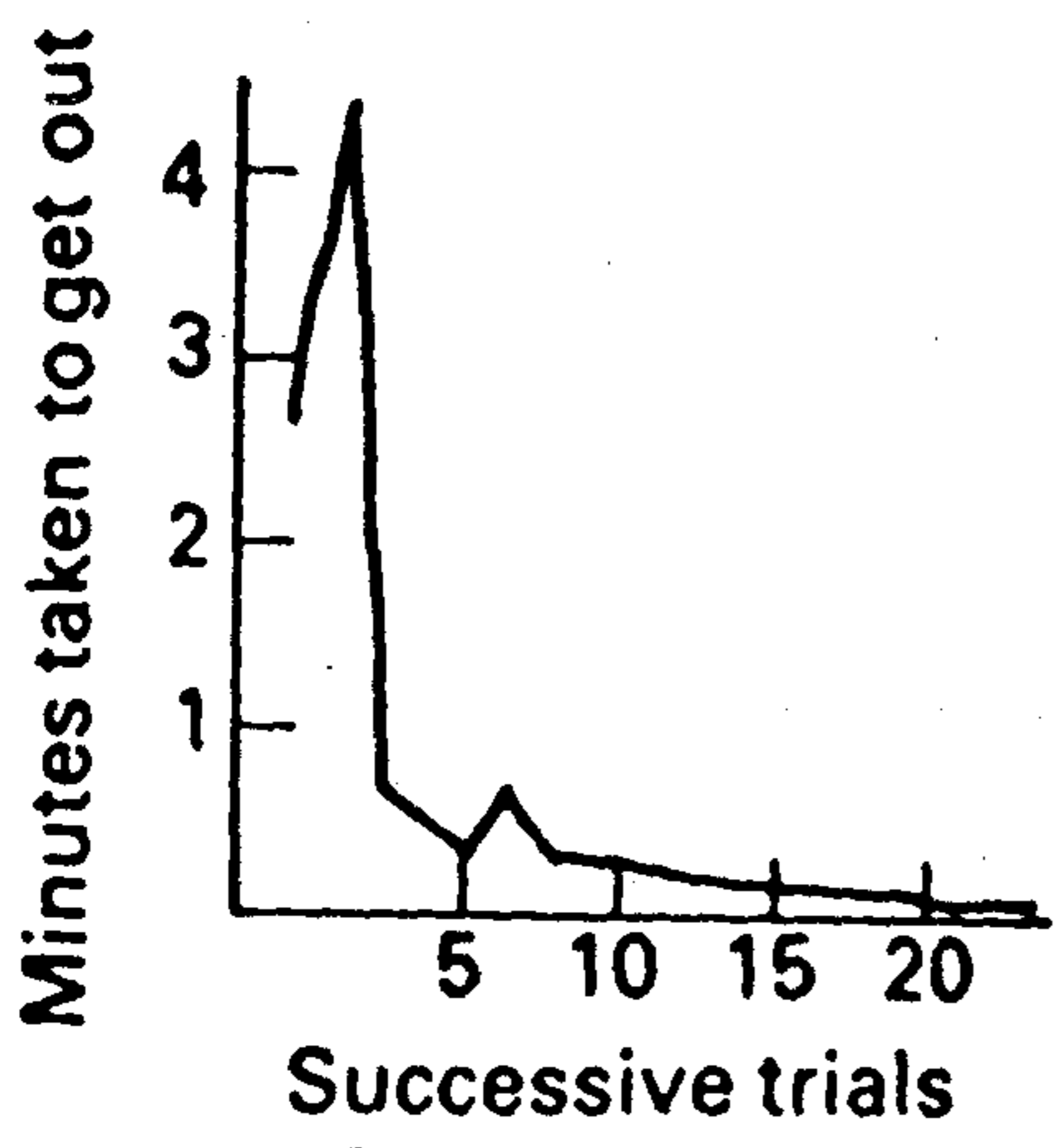


Figure 5.2 *Thorndike's results.*
See text. After Thorndike (1898).

both figures
from Walker (1987)

INSTRUMENTAL CONDITIONING

Thorndike (1898,1901) Hull (1943) Skinner (1938,1977)	Versus	Tolman (1932,1948) Mackintosh (1983) Rescorla (1990,1991)
Minimum cognition Stimulus-Response Habits No reward anticipation		More cognition “Cognitive maps” of the spatial environment “Expectancies” of reward

EVIDENCE FOR TOLMAN WINNING

- **Tinkelpaugh (1928): disappointment of expectancies**
- **Spatial Learning: Tolman and Honzik (1930a – sheet 15)**
- **Reward Re-evaluation**
 - a. Latent learning (Tolman and Honzik, 1930b --see overheads) After learning a maze with no reward, performance improve immediately reward is introduced.
 - b. The radial maze (Olton and Samuelson, 1976): rats do not repeat rewarded actions if these involve going to multiple locations which each contain one food pellet.
 - c. Crespi (1942 – see overhead). After learning to run down an alley for a large reward, speed of running reduces immediately when the size of the reward is reduced. (See also Dickinson, 1985; Rescorla, 1991)

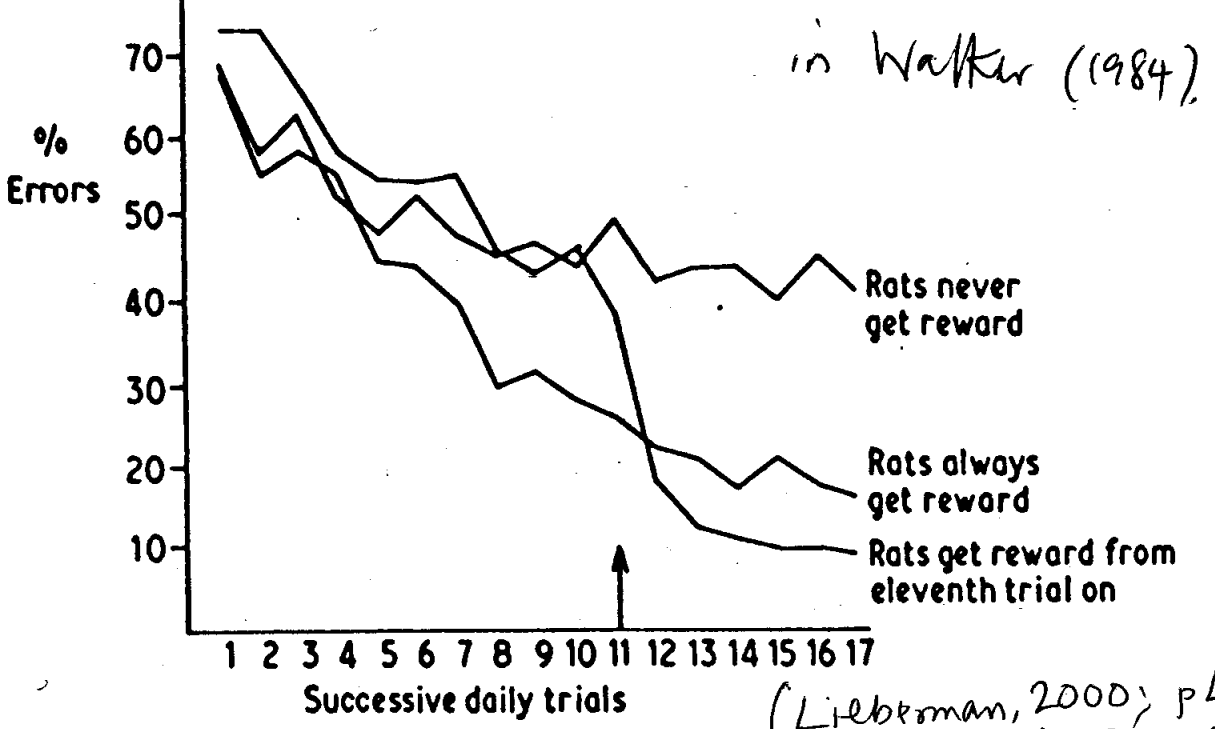
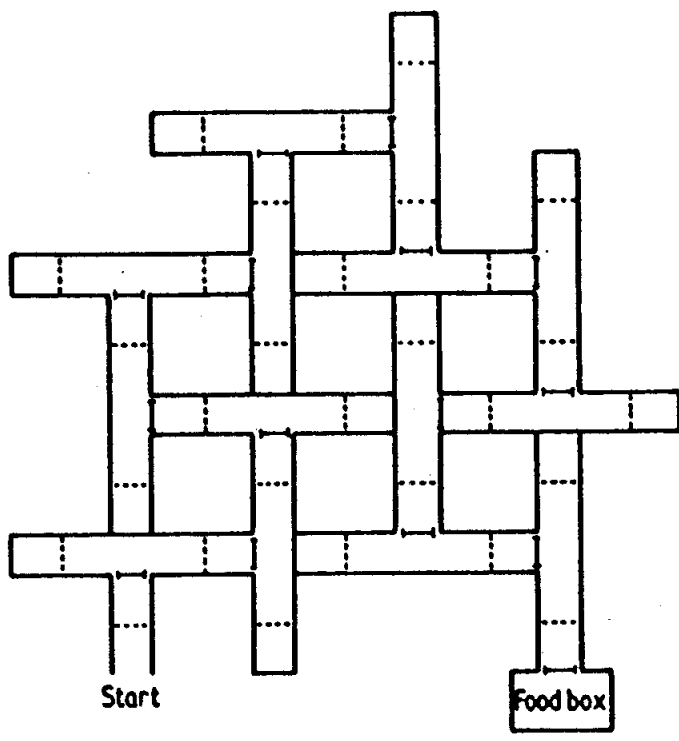


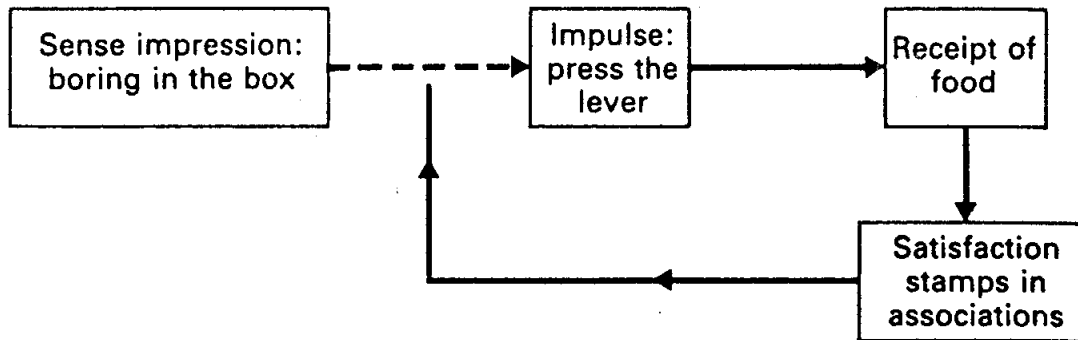
Figure 2 Latent learning results.

The obvious way of getting a rat to learn a maze is to provide it with a food incentive at the end. Rats always rewarded in this way show a gradual decrease in errors (turning the wrong way in a maze like that shown in figure 1). Rats who are never rewarded continue to make many errors. But animals run initially without any food incentive (in this case for the first ten days), who have apparently learned nothing, show an immediate improvement in performance after just one reward, proving that some learning had taken place on the non-rewarded trials, even though this was not obvious in the rats' behaviour until rewards were given. (After Tolman and Honzik, 1930)

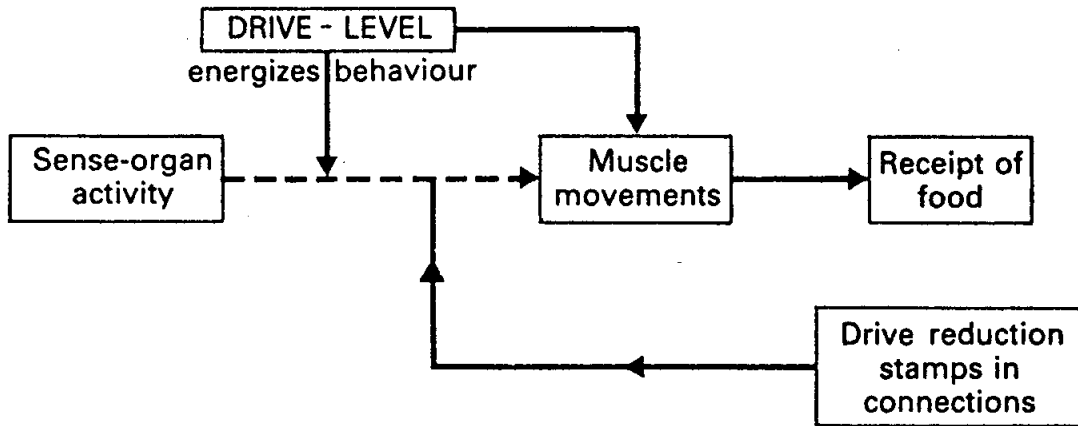


.... curtains
 → doors

(a) Thorndike : impression-impulse associations



(b) Hull : receptor-effect or stimulus response connections



(c) Pavlov/Tolman: stimulus-reward and response-reward associations

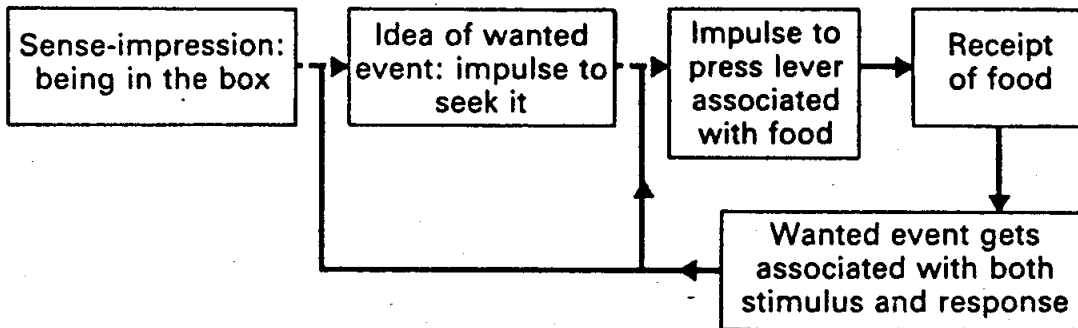


Figure 5.7 Theories of instrumental learning.
See text.

is in part indirect, in the form of evidence *against* stimulus-response principles, and in part more positive, in the form of evidence that an evaluation of goals determines instrumental performance and that responses become associated with consequent rewards.

his theory (though not to abandon drive reduction altogether) suggested that even the physical properties of reinforcing agents themselves do not adequately predict their behavioural effects, but rather, an internal evaluation of a given reward determines its effects on the learned performance of hungry rats. Crespi (1942) compared the performance of rats trained to run down an alley for food rewards of just less than a third of a gram with that of groups trained first with larger or smaller rewards, and then shifted to this reward amount. Figure 5.3 illustrates the case of rats which first experienced

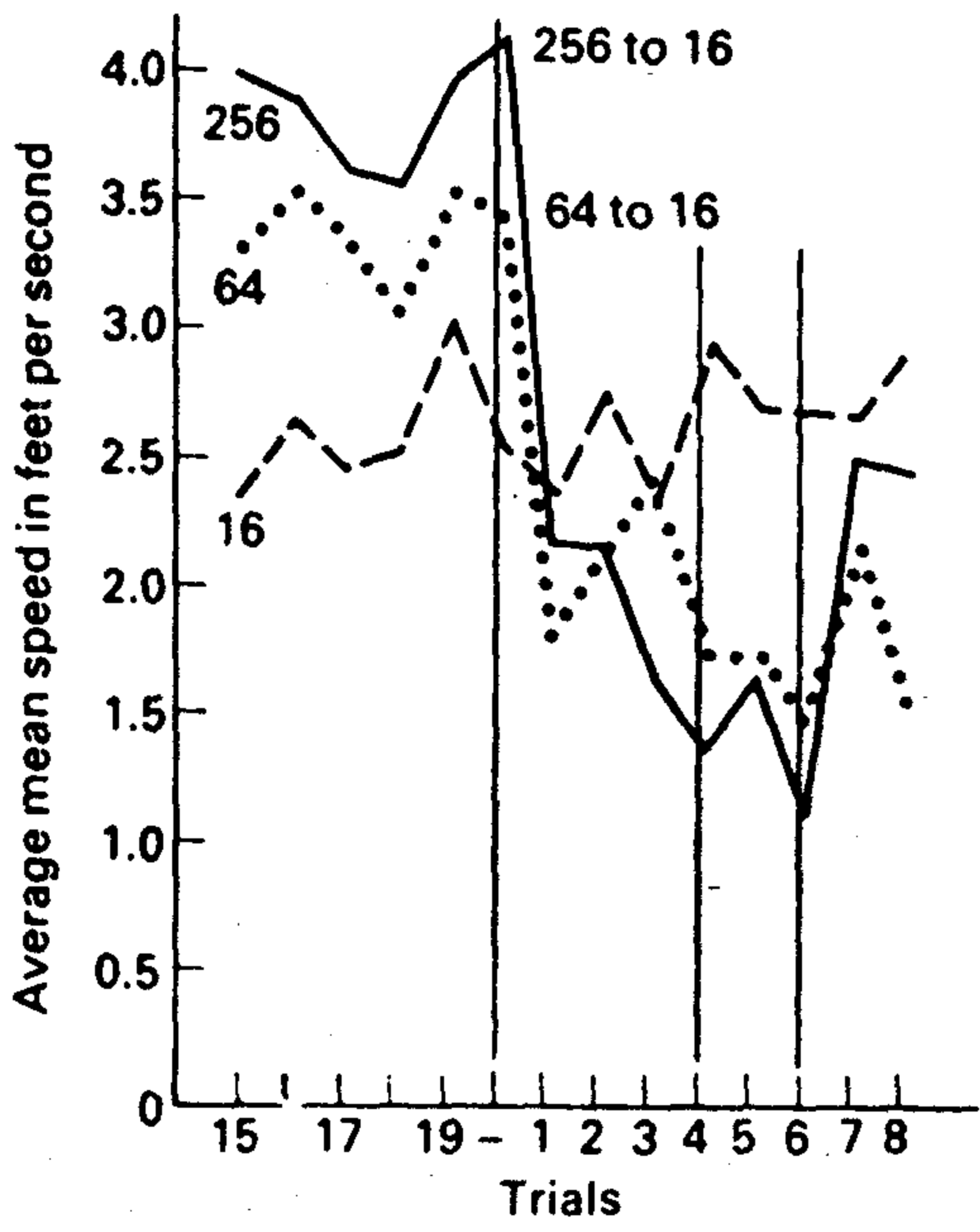


Figure 5.3 The emotional effects of rapid incentive learning. Results of an experiment in which the amount of food obtained as reward by rats for running to the end of a straight alley was varied, using units of a 50th of a gram. Rats trained with larger rewards ran faster than rats trained with a small reward, but when all then received that small reward, a rapid reduction in speed of running took place in those rats which had formerly been given large rewards, so that they ran more slowly than rats already accustomed to receiving small rewards. After Crespi (1942).

see Liberman (1993) page 229
or (2000) page 231

From Walker (1987) page 173

(See also Lieberman, 1993/2000 “Reinforcement and conditioning: One process or two? page 343/442)

Either:

There is one kind of learning process underlying both Pavlovian and Instrumental conditioning.

Just Classical (Pavlov, 1927; Spence, 1956; Moore, 1973; Dickinson, 1980; Lieberman, 1993, 2000)

Just Instrumental (Hull 1943; Perkins, 1968)

Or:

There are two kinds of process, and many natural and laboratory forms of learning involve both of them. This is “two-process” or “two factor” theory. (Konorski and Miller, 1937; Skinner, 1938; Gray, 1975; Mackintosh, 1974, 1983; Walker, 1987; Rescorla, 1991, 1994)

Skinnerian “Schedules of Reinforcement”

(Ferster and Skinner, 1957; see Lieberman, 1993/2000, pp. 215-255/220-229)

Continuous Reinforcement (=CRF; =FR1)

A reward is given after every response.

Fixed Ratio (FR)

A reward is given after every n responses (e.g. 10)

Variable Ratio (VR)

A reward is given after every n responses (e.g. 10) on *average*, but the exact number of responses is unpredictable.

Fixed Interval (FI)

A reward is available for just one response, but only after a fixed time (e.g. one minute) has elapsed since the last reward.

Variable Interval (VI)

A reward is available for just one response, but only after an unpredictable amount of time has elapsed (n minutes on average) since the last reward.

at a time, w
reach.
As a prere
be adapted
tomed to eat
A hungry bi
as possible w
able for only
waste no tim
signalled by
of the hoppe
discriminative
Now the very
behaviour pa
studied respo
a strong peck
records the r
To persuade
approximation
and make a s
earn a few se
menter might
activate the m
few inches of
dramatic effec
quired by the
Now the exp
movement tov
This results i
the criterion f
peck. Sooner o
button itself, a
if it gains a sm
Although, as
ing is an easy
response-shapi
wide variety o
powerful enoug
major tool in
by operant me
of prompting
method of teach

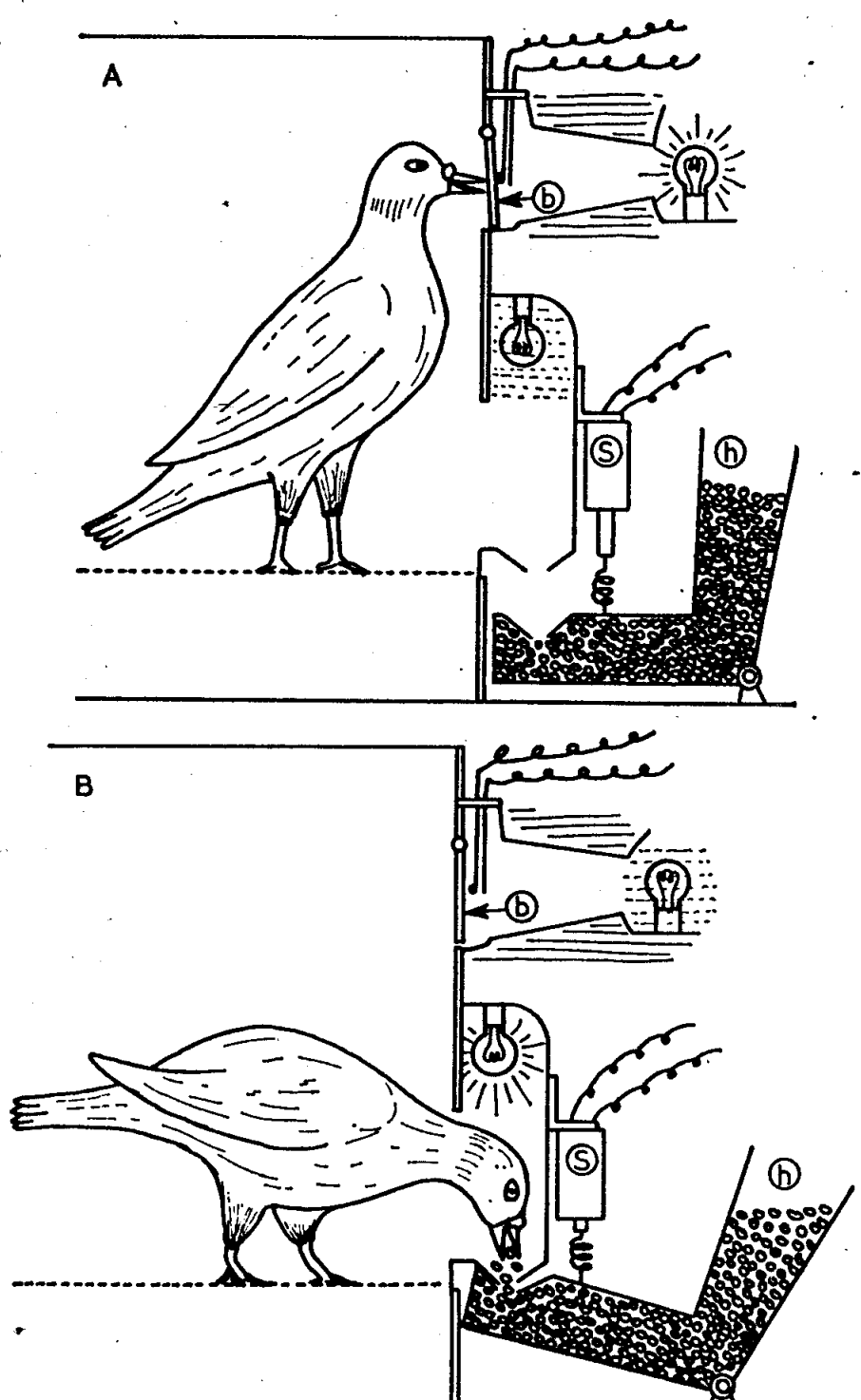


Fig. 4.1 Operant conditioning apparatus for pigeons. In A the bird has just made contact with the pecking button (b). In B this peck is reinforced: current is supplied to a solenoid (s) which lifts up the grain hopper (h) for a few seconds. (After Ferster and Skinner, 1957)

14

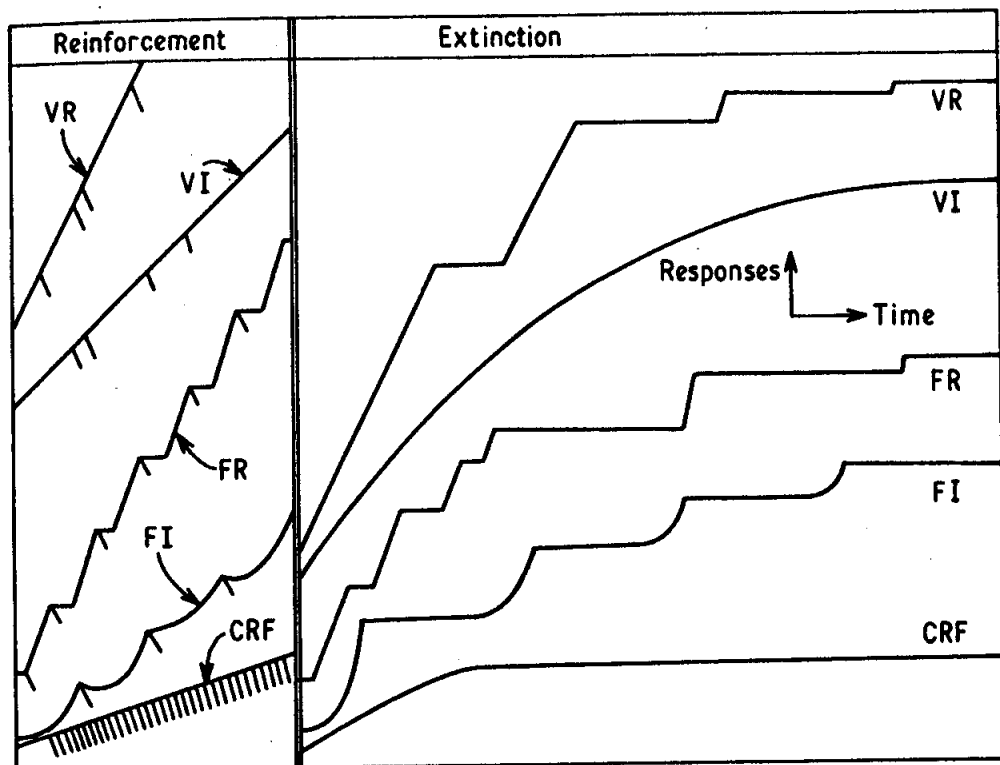


Figure 4 Cumulative records of reinforced responding and extinction with basic schedules of reinforcement.

reward can be obtained must be unpredictable, and a steady and fast rate of response is eventually obtained, indicating either that the animal expects reward at any time or that consistent and sustained patterns of responding have become habitual. There is still a slight tendency for response rate to increase as time passes since the last reinforcement. When all reinforcements are discontinued, response rate declines very slowly and gradually.

4 *Fixed-ratio schedules*: care is necessary for training on fixed-ratio schedules. The rule is that the animal must make a certain fixed number of responses for each reward. An animal first reinforced for every response, and then put immediately on the task of making a hundred responses per reward (FR₁₀₀) would almost certainly give up. However, suppose that the task requirement is increased gradually, or that, as in Skinner's original experiment (1938), the animals are first trained on an interval schedule (which allows for backsliding because rewards are always available at some point for just one response). In this case ratios of tens or hundreds may be undertaken by rats and pigeons, and a ratio of

“Optimal foraging”

15

Animals are often assumed to behave in ways which maximize their net rate of energy intake (Davey, 1989, p237).. Other models of optimality are possible. In many cases species must use learning and memory in order conform to the rules of optimality models. They must also use judgements about the relative merits of various goal objects, which is different from just controlling behaviour by Thorndikean changes in the strength of motor response outputs.

Choice between better and worse prey items

It is deduced that the choice should be influenced by the availability of the most preferred item, but not by the availability of the least preferred item. (p241)

This has been checked with shorebirds in the field (redshank) choosing large or small worms (Goss-Custard, 1977) and pigeons choosing immediate or delayed rewards in the laboratory (Lea, 1979)

Choosing where to forage (“Patch selection”)

One theory (the “marginal value theorem”) says that an animal should leave a particular patch when its energy intake drops to the average level for the surrounding habitat. This involves the concept of an “expected rate of return”. (Davey, 1989; p245).

HARPER (1982): data discussed in GALLISTEL (1990)
“The Organization of Learning” Chapter 11

358

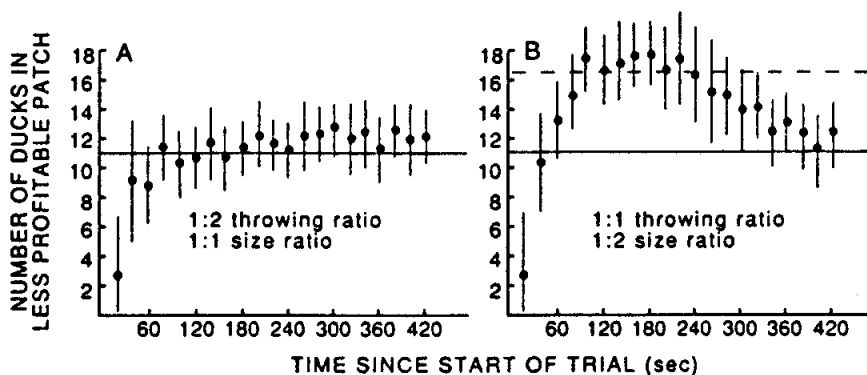


Figure 11.3.

The mean numbers of ducks in front of the thrower providing the least food per unit time, as a function of the time since the onset of throwing. The solid horizontal lines indicate the apportionment that accords with the relative rate of food provision. The dashed horizontal line in B indicates the apportionment that corresponds to the relative rates of throwing, not taking into account that one thrower is throwing chunks twice as big. Vertical bars are standard deviations. A. Data from eleven trials in which equal-sized pieces of bread (2 grams) were thrown, but the less profitable thrower threw half as often. B. Data from fourteen trials in which the throwers threw equally often, but the more profitable thrower threw 4-gram chunks instead of the usual 2-gram chunks. (Modified from Harper 1982, p. 582, by permission of author and publisher.)

suggests that birds accurately represent rates, that they accurately represent morsel magnitude, and that they can multiply the representation of morsels per unit time by the representation of morsel magnitude to compute the internal variables that determine the relative likelihood of their choosing one foraging patch over the other.

16. Baum, 1974; Kachlin *et al.*, 1981; Prelec, 1982, 1984; Shimp, 1969; de Villiers and Herrnstein, 1976). For present purposes it is sufficient merely to stress that the regularity does not arise only because a response is strengthened in proportion to the exact number of times it is rewarded.

There is a descriptive generality, called the 'matching law', which can be given either as

$$\frac{B_1}{B_1 + B_2} = \frac{R_1}{R_1 + R_2} \quad (1)$$

or as

$$\frac{B_1}{B_2} = \frac{R_1}{R_2} \quad (2)$$

where B_1 and B_2 are the absolute frequencies of two behaviours, and R_1 and R_2 are the absolute numbers of rewards each receives per hour. There are two general kinds of explanation for why this equation satisfactorily predicts behaviour, and therefore predicts in some sense the choice that a pigeon makes between two responses. The first kind says that the matching law arises because in some way or other animals are very efficient, as it happens close examination of what the two theories predict about experimental results suggests that they are 'empirically indistinguishable' (Ziriax and Silberberg, 1984; see Mackintosh, 1983, p. 258).

Relative reward value

There is, however, an extremely unambiguous empirical distinction between two possible rules which would both produce the matching law in practice. One rule implies that any response is performed according to the reinforcements it itself receives; the other says that a response is performed according to the *relative* value of the reinforcements it receives – most directly according to the proportion of the total rewards that are assigned to it in circumstances of choice. Thus

$$B_1 = kR_1 \quad (3)$$

is the first case and

$$\frac{B_1}{R_1 + R_2} = k \quad (4)$$

is the second. Either equation (3) or equation (4) would

DEFINITION OF AN OMISSION PROCEDURE

Normal classical conditioning

CS → UCS
CS+CR → UCS

e.g

light → FOOD
light+saliva → FOOD

Classical conditioning with omission

CS → UCS
CS+CR → **NO UCS**

e.g. Williams and Williams, 1969

light → FOOD
light+peck → **NO FOOD**

With this omission procedure, the Pavlovian effect of anticipatory conditioned responding is pitted against the instrumental influence which would suppress responding in order to maximise goal achievement. Williams & Williams (1969) found that pigeons would miss up to 50% of possible food rewards.

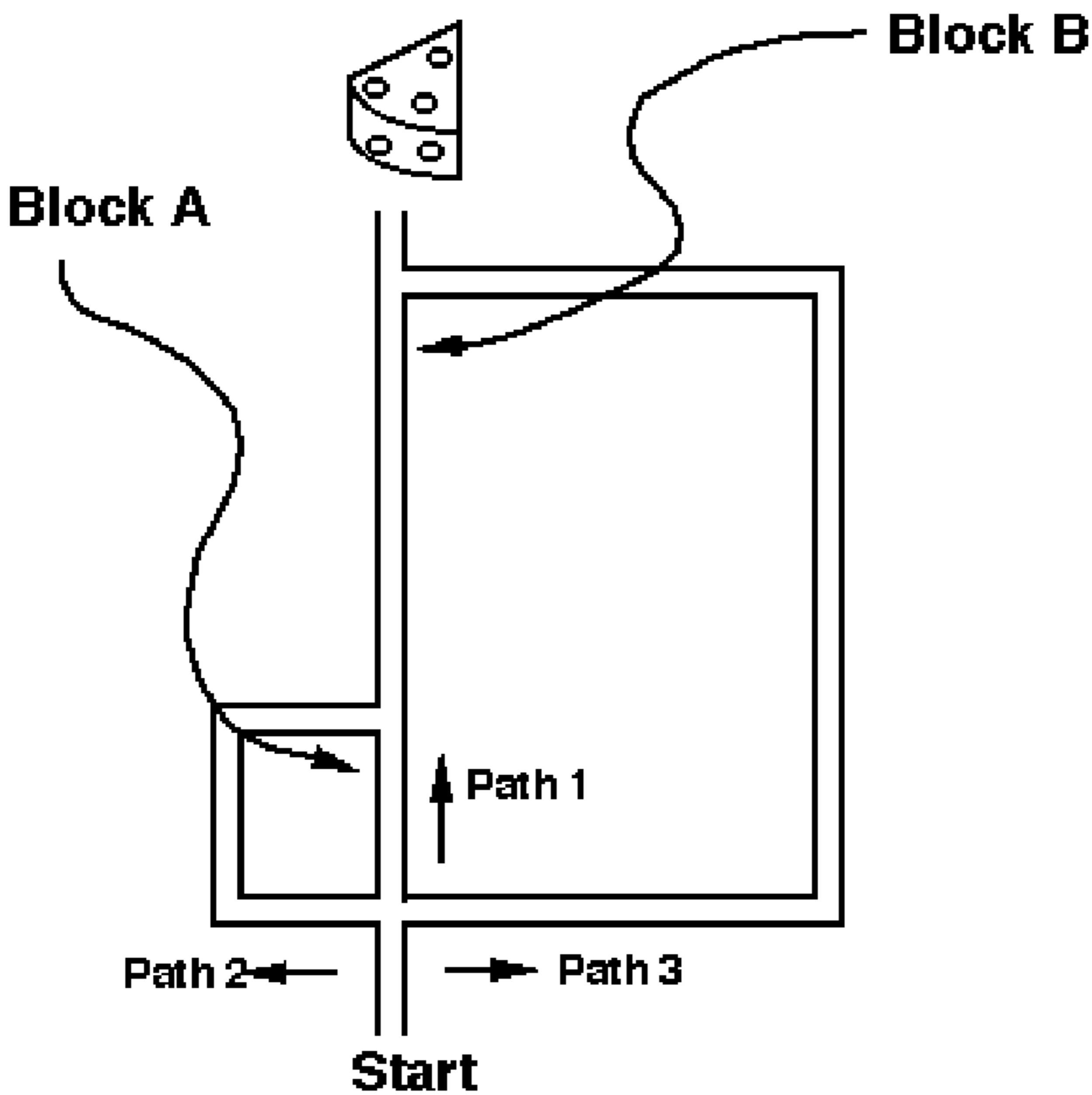
(With an aversive UCS, the instrumental influence should enhance responding in an omission procedure. This is avoidance training, where it is clearly more difficult to separate Pavlovian and Instrumental effects, but where both undoubtedly can occur.)

Contrasting Features of Classical and Instrumental Conditioning

	CLASSICAL	INSTRUMENTAL
1.	Applies to the Autonomic Nervous System and reflexive motor responses.	Does not apply to the ANS. Works with learned motor skills, response strategies and goal-directed actions.
2.	There is usually very little internal feedback from ANS responses.	There is plenty of internal and external feedback for skeletal motor responses.
3.	Primarily concerns learning of relations between stimuli.	In the first instance concerns learning of motor responses
4.	Typically applies to involuntary responses.	Can apply to voluntary responses where this can be assessed.
5.	Is "drive inducing" i.e. in conditioning of emotional effects emotional changes are brought about by conditioning.	Is "drive reducing", i.e. achieving goals reduces drives, and according to the Law of Effect, learning is caused <i>by</i> emotional changes.
6.	Characteristically uninfluenced by motivational pay-offs. i. Effects are insensitive to omission schedules. ii. In some cases (knee jerk, some metabolic responses and perceptual responses, the UCS may have little motivational value.	Almost by definition sensitive to emotional pay-offs. A variety of relations between response effort or response cost and the response outcomes are possible.
7.	Intermittent or unreliable relations between the CS and UCS weakens conditioned effects, especially with attractive motivational stimuli.	Intermittent and unreliable relations between the learned response and the motivational pay-off may strengthen the learned behaviour.

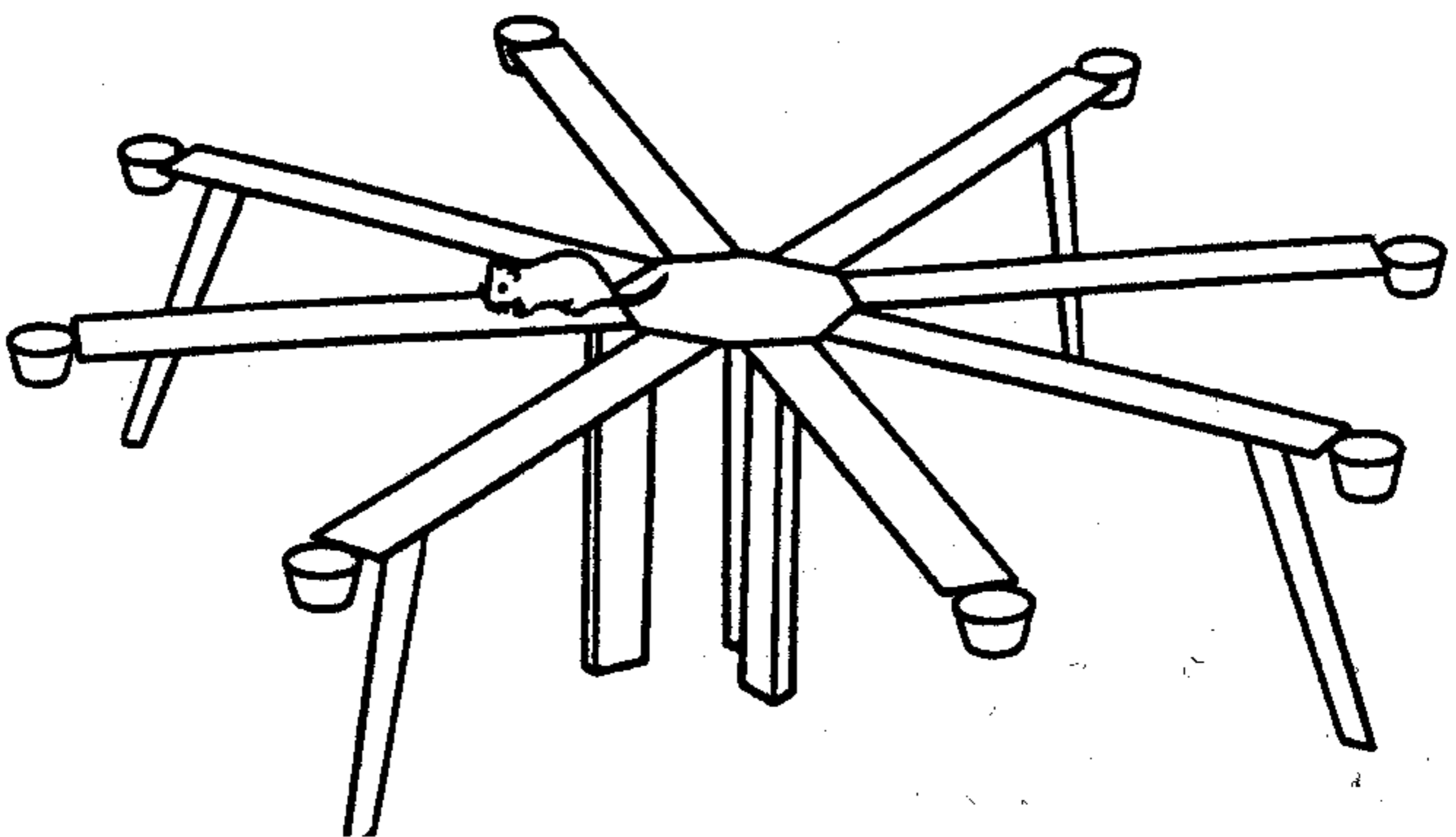
Shared Features of Classical and Instrumental Conditioning

1.	Experimental procedures frequently make use of the same motivating conditions, e.g. hungry animals receiving food.
2.	Course of learning in both cases includes acquisition, extinction, and discrimination of stimuli which are and are not associated with motivationally significant events.
3.	Results with both procedures show that the innate predispositions of particular species influence the outcomes of the procedures..



19

Maze used by Tolman and Honzik (1930a), in a paper about "insight". If rats are allowed to move from the start box to the goal box by which ever route they choose then the 3 paths are all tried out, but with experience preferences are established according to length. If path 1 is blocked at A then rats go back and choose path 2, which could be a simple example of this preference. If however path 1 is blocked at B, then 9 out of 10 of the rats in this experiment chose path 3. This is the longest, but the only effective way of avoiding the block at B. Tolman used this sort of evidence in favour of his suggestion that rats form "cognitive maps". A reproduction of the original figure is given in Lieberman (1993/200, page 489/353)



A drawing of a rat on an 8-arm radial maze. There is a food cup at the end each arm, containing one food pellet, out of sight. After several days' training, rats on average choose about 7.5 novel arms in their first 8 choice. The usual assumption is that they have some form of memory for where they have already been on a given day, and avoid retracing their steps.

This is well above chance. With a 17-arm maze, they typically choose 14 different arms in the first 17 choices. Test show that this depends on visual landmarks rather than odour, since confining the rat, under a cover, in the central platform, between choices, while the experimenter exchanges an arm already explored with one which has not been used on that day, shows that rats will explore an arm which has already been visited, if it is in a new geographical position. (See Walker, 1987; p. 144 & Lieberman, 2000; p.382).

SUB-TOPICS

Pleasure-Seeking Behaviour

Pleasure and Drugs



Just beside the ventral tegmental area is another part of the brain that contains a great deal of dopamine: the substantia nigra. The dopaminergic neurons of the substantia nigra project their axons into the corpus striatum, a region associated with the control of movement.

Essentially all of the dopamine that modulates brain activity comes from the ventral tegmental

SUB-TOPICS

Pleasure-Seeking Behaviour

Pleasure and Drugs



The behaviours that the reward circuit drives us to repeat

as in the case of a drug dependency, can be reinforced positively or negatively.

In a **positive reinforcement**, the motivation for seeking the substance is the pleasure that it provides. In a **negative reinforcement**, the motivation is to relieve a physical discomfort, a depressive state, or social isolation.

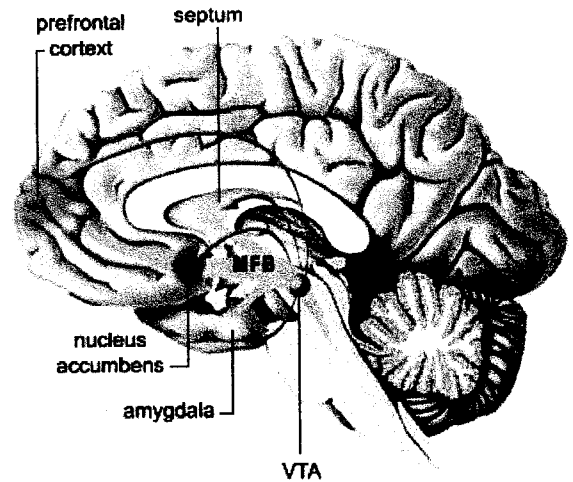
Various theories explaining dependency behaviours posit that both types of reinforcement could be at play simultaneously to differing extents.

THE PLEASURE CENTRES

When the cortex has received and processed a sensory stimulus indicating a reward, it sends a signal announcing this reward to a particular part of the midbrain—the **ventral tegmental area (VTA)**—whose activity then increases. The VTA then releases **dopamine** not only into the **nucleus accumbens**, but also into the **septum**, **the amygdala**, and the **prefrontal cortex**.

The nucleus accumbens then activates the individual's motor functions, while the prefrontal cortex focuses his or her attention.

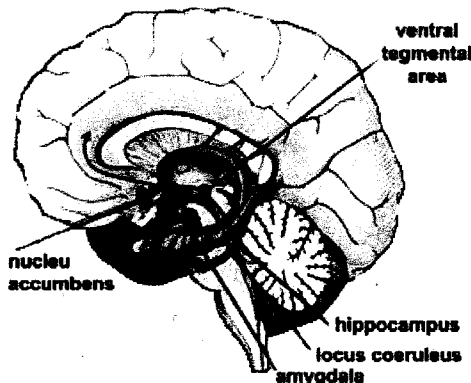
These regions are connected by what is called the pleasure or reward bundle. In neuroanatomical terms, this bundle is part of the **medial forebrain bundle (MFB)**, whose activation leads to the repetition of the gratifying action to strengthen the associated pathways in the brain.



THE PLEASURE CENTRES AFFECTED BY DRUGS

The nucleus accumbens definitely plays a central role in the **reward circuit**. Its operation is based chiefly on two essential neurotransmitters: **dopamine**, which promotes desire, and **serotonin**, whose effects include satiety and inhibition. Many animal studies have shown that all drugs increase the production of dopamine in the nucleus accumbens, while reducing that of serotonin. * of abuse

But the nucleus accumbens does not work in isolation. It maintains close relations with other centres involved in the mechanisms of pleasure, and in particular, with the **ventral tegmental area (VTA)**.



Located in the midbrain, at the top of the brainstem, the VTA is one of the most primitive parts of the brain. It is the neurons of the VTA that synthesize dopamine, which their axons then send to the nucleus accumbens. The VTA is also influenced by endorphins whose receptors are targeted by **opiate** drugs such as heroin and morphine.

Another structure involved in pleasure mechanisms is the **prefrontal cortex**, whose role in planning and motivating action is well established. The prefrontal cortex is a significant relay in the reward circuit and also is modulated by dopamine.

The locus coeruleus, an alarm centre of the brain and packed with norepinephrine, is another brain structure that plays an important role in drug addiction. When stimulated by a lack of the drug in question, the locus coeruleus drives the addict to do anything necessary to obtain a fix.

Two structures in the limbic system also play an active part in the pleasure circuit and, consequently, in drug dependency. The first is the **amygdala**, which imparts agreeable or disagreeable affective colorations to perceptions.

The second is the **hippocampus**, the foundation of memory, which preserves the agreeable memories associated with taking the drug and, by association, all of the details of the environment in which it is taken. Sometime in the future, these details may reawaken the desire to take the drug and perhaps contribute to recidivism in the patient.