PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Introduction: Categorization, Cleverness and Consciousness

L. Weiskrantz

Phil. Trans. R. Soc. Lond. B 1985 **308**, 3-19
doi: 10.1098/rstb.1985.0006

Phil. Trans. R. Soc. Lond. B **308**, 3–19 (1985) [3]
Printed in Great Britain

Introduction: categorization, cleverness and consciousness

By L. Weiskrantz, F.R.S.
Department of Experimental Psychology, South Parks Road, Oxford OX1 3UD, U.K.

[Pullout 1]

Various recurring themes in the history of the subject are reviewed. In the context of adaptation to a complex environment, one precondition for survival must be a capacity for object identity, which may be the most basic form of categorization. Evidence will be presented that suggests that the capacity is not learned. In considering learned associations among categorized items, a distinction is made between reflexive and reflective processes: that is between those associations in which a cue or signal provides an unambiguous route to the response, no matter how complex that route may be, in contrast to those in which learned information must be ordered and reordered 'in thought'. An example of one experimental approach to the latter is provided. Finally, the problem of conscious awareness is considered in terms of stored categorical knowledge and associations, on the one hand, and a system that monitors them, on the other. Neurological evidence of disconnections between these different levels is reviewed.

1. Historical contrasts over the past 100 years

Given the uncertainty, not to say controversy, that the term '*human* intelligence' provokes these days, there may well be a question about the profitability of discussing '*animal* intelligence'. 'What', asked Fabre, the great French naturalist, 'is human intelligence? In what respect does it differ from animal intelligence? What is instinct? Are these two mental aptitudes irreducible, or can they both be traced back to a common factor?... These questions are, and always will be, the despair of every cultivated mind, even though the inanity of our efforts to solve them urges us to cast them into the limbo of the unknowable' (Fabre 1919, p. 107). But, in spite of this, there is no doubt that for the past 100 years there has been almost an obsessional interest in discovering or uncovering the mental capacities of non-human creatures, or 'brutes' as they were called until about the turn of the century.

The floodgates were opened by many, but no doubt Darwin must take the main responsibility because the revolution he spawned made it necessary to consider the continuity between ourselves and other creatures. Given that we have mental capacities, it seemed reasonable not only to ascribe them to animals but to enquire into their relative development, and Darwin, while acknowledging that 'the difference between the mind of the lowest man and that of the highest animal is immense', was, nevertheless, convinced that the difference 'certainly is one of degree and not of kind. We have seen that the senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason, etc., of which man boasts, may be found in an incipient, or even sometimes in a well-developed condition, in the lower animals' (*Descent of Man* (Darwin 1871), pp. 125–6). Darwin with the passage of time appears to have become more confident of this congenial conclusion: in the *Origin of species*, some 14 years earlier (Darwin 1859), he allowed only that 'a little dose of judgment or reason often comes into play, even with animals low in the scale of nature' (p. 266). Earlier writers (and even some later ones, such as Jacques Loeb, who resisted the flood), could be mechanistic, in the literal sense, about animals, as was Descartes. John Locke (1690), while not quite relegating animals to the level of bare machines, nevertheless was 'positive...that the power of abstracting is not at all in them; [it is] an excellency which the faculties of brutes do by no means attain to' (1690, vol. 1, p. 126). Fabre, Charles Darwin's contemporary (1916, chapter vii) scornfully and mercilessly demolished a putative observation of 'reason' in the wasp by Erasmus Darwin and would not allow insects even the 'little dose of reason' that Charles Darwin was prepared to admit.

From Darwin derives not only the explicit assumption of animal–human continuity, but also the implicit assumption that behaviour patterns, from which intelligence must be inferred, are proper candidates for evolutionary selection, a tenet that became the foundation stone of ethology and was also seminal for many branches of psychobiology. In one of his notebooks Darwin wrote that 'he who understands baboon would do more towards metaphysics than Locke' (Notebook M, p. 84, 16 August 1838; cf. Gruber (1974) pp. 317–318). Darwin himself, however, is relatively silent, even impotent, when it comes to those behavioural descriptions that might lead to a deep or systematic understanding of the cognitive capacities of animals, let alone metaphysics, and his most concentrated treatment of reasoning, for example, in the *Descent of man* is little more than scattered anecdotes of doubtful value. His observational methods, so well adapted to the analysis of 'natural' and conspicuous forms of behavioural display in *The expression of emotions in man and animals*, fail lamentably when applied to the drawing of inferences about cognition. In writing about 'reflection', for example, he remarks that 'Australians, Malays, Hindoos, and Kafirs...frown, when they are puzzled. Dobritzhoffer remarks that the Guaranies of South America on like occasions knit their brows. From these considerations, we may conclude that frowning is not the expression of simple reflection, however profound, or of attention, however close, but of something difficult or displeasing encountered in a train of thought or action. Deep reflection can, however, seldom be long carried on without some difficulty, so that it will generally be accompanied by a frown' (1965 edition, p. 222). He goes on to describe how he generated such a state in some unwitting volunteers by 'making them believe that I only wished to test the power of their vision'. He proceeds to even more difficult realms – 'abstraction' and 'meditation': 'The vacant expression of the eyes is very peculiar, and at once shows when a man is completely lost in thought.' He recruited Professor Donders into measuring the divergence of the eyes in such a state, 'if the eyes be held vertically, with the plane of vision horizontal, amounting to 2° as a maximum'. His description then goes on very precisely concerning the greater degree of divergence, up to 3° 5′, as the head droops, and the eyes are turned a little upwards, and 6° or 7° if the eyes are turned still more upwards. He concludes the section by remarking that 'we can understand why the forehead should be pressed or rubbed, as deep thought tries the brain; but why the hand should be raised to the mouth or face is far from clear' (p. 228).

'It is something to observe', said Fabre (on whom Darwin admiringly bestowed the title of 'incomparable observer', but who was for his part an unremitting critic of Darwin, referring to him sardonically as 'O illustrious master'), 'but it is not enough: we must experiment, that is to say, we must ourselves intervene and create artificial conditions which oblige the animal to reveal to us what it would not tell if left to the normal course of events...To bring out the truth, we must resort to experiment, which alone is able to some extent to fathom the obscure problem of animal intelligence...Observation sets the problem; experiment solves it, always

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

presuming it can be solved; or at least, if powerless to yield the full light of truth, it sheds a certain gleam over the edges of the impenetrable cloud' (1919, pp. 108–9). The Darwinian revolution made it permissible, even compulsory, to consider animal cognition, but without itself providing the methods for pursuing the matter. But others were not slow to try to find them. This cannot be the place for a review of this quite fascinating history, starting perhaps with Fabre himself, then George John Romanes, Darwin's friend and ardent admirer, the equally ardent Lloyd Morgan, and that remarkable intrepid experimentalist, L. T. Hobhouse who anticipated much of Köhler's and Yerkes' line of thinking, and also helped to put 'Mr' Thorndike in his place (Lloyd Morgan, who was well disposed to Thorndike's approach, always addressed him as 'Professor'), and H. S. Jennings. The history is very rich, and deserves a good review, but I will have time only to refer to illustrative bits as we turn to other matters.

In holding a meeting today on such a topic, we must try to see how the scene has changed over the past 100 years. One point that ought to be made straight away is that in many ways it has not changed: issues discussed today were discussed just as earnestly and perspicaciously 100 years ago. Thus, we have much flurry today about 'intentionality' as applied to animal behaviour (cf. Dennett 1983) but Jennings in 1905 made a very similar point, with infinitely more empirical experience of the subject than modern philosophers, when he remarks that 'we usually attribute consciousness...because this is useful; it enables us practically to appreciate, foresee, and control [an animal's] actions much more readily than we could otherwise do so'. The anti-intentionality writers also have their historical forebears: Pavlov wrote, 'in our "psychical" experiments on the salivary glands at first we honestly endeavoured to explain our results by fancying the subjective condition of the animal. But nothing came of it except unsuccessful controversies, and individual, personal, uncoordinated opinions' (1928, p. 50).

There is also the same debate between 'rules' and 'reference' in earlier writers' distinction between 'practical learning' and 'rationality' (for example, Lloyd Morgan 1900; Hobhouse 1901). Earlier writers were also not unconcerned with the question of use of tools, as in the cebus monkey of Romanes, whose sister observed it cracking nuts with a hammer (an observation that Hobhouse could not confirm himself with his own monkeys), and Darwin in *Descent of Man* cited a number of positive claims of tool use by apes, monkeys, and elephants. ('The tamed elephants in India are well known to break off branches of trees and use them to drive away the flies; and the same act has been observed in an elephant in a state of nature', p. 81.)

Needless to say, there was also the same debate about whether animals understood words in isolation, or had some linguistic comprehension. Darwin concluded that 'that which distinguishes man from the lower animals is not the understanding of articulate sounds, for, as every one knows, dogs understand many words and sentences. In this respect they are at the same state of development as infants, between the ages of 10 and 12 months, who understand many words and short sentences, but cannot yet utter a single word (*Descent of Man*, p. 85). But Lloyd Morgan writes wryly that 'when I said "whiskey" to my fox-terrier, he would at once sit up and beg; not because his tastes were as depraved as those of his master, but because the *isk* sound, common both to "whiskey" and "biscuit", was what had for his ears the suggestive value' (1900, p. 203). Later he remarks 'the animal "word", if we like so to term it, is an isolated brick: a dozen, or even a couple of hundred such bricks do not constitute a building, be it a palace or only a cottage; hen language, or monkey language is, at best, so far as we at present have evidence, an unfashioned heap of bricks'. In an earlier work (1890) he put the now familiar epistemological point that [whilst] 'the actions of the speechless child and our dumb companions show that they...are capable of forming mental products of the perceptual order,...we must not forget that we interpret the percepts of children and animals; that in so doing we cannot divest ourselves of the garment of our conceptual thought, that we cannot banish the Logos, and that, therefore, these percepts other than ours cannot be identical with ours, though they are of the same order, saving their conceptual element. We may put the matter thus:

$$\left.\begin{array}{ll}(1) & x \times \text{dog-mind}\\ (2) & x \times \text{cat-mind}\\ (3) & x \times \text{infant-mind}\end{array}\right\} = \left\{\begin{array}{l}\text{percepts to be interpreted in terms of (4), being}\\ \text{analogous thereto but not identical therewith}\end{array}\right.$$

(4) $x \times$ adult human mind = the percepts of psychologists, named or nameable.

Nor were writers of the time unaware of the powerful dangers of imitation in yielding misleading 'Clever Hans' types of results: Hobhouse (1901) has a lengthy and detailed review of the importance of the presence of the experimenter in a variety of such claims. And given modern interest in sequential runs of behaviour, the earlier concern with 'counting' by birds, and the recognition of its importance, is worth noting. Interestingly, Romanes wrote at great length about the subject in a letter to *The Times* (19 September 1888), both about rooks and about his own observations on a chimpanzee (which, if true, makes a chaining explanation impossible). The similarity to interpretations of much more recent experiments on birds by, for example, Koehler (1951), is striking. This use of the medium of *The Times* for interpreting animal behaviour, incidentally, is by no means past: provoked by an account in that paper on 20 October 1981 of the study by Woodruff and Premack that reported, among other things, that the chimpanzee Sarah was 'the first non-human to be accused of lying', two days later no less a person than a past President of the British Academy, Sir Kenneth Dover, drawing on the authority of Robert Louis Stevenson, wrote in a letter to *The Times* that 'all intelligent dogs are accomplished and incorrigible liars'. A little before that (21 October 1971), the following letter from a titled lady appeared in that same paper.

> From articles and lectures by experts, I have always understood that dogs have no colour sense. The following incident may therefore be of interest to professional and amateur alike.
>
> Our Labrador dog (11 years old), has shown no interest whatsoever in black and white television. We have recently acquired a colour set, since when he sits gazing at the screen for lengthy periods. This afternoon he watched Mrs Margaret Thatcher addressing the Conservative Party Conference. She was wearing the conference badge (in colour red) and after watching for a short time, he went up to the screen and licked the exact spot where the red badge was showing.
>
> Our dog has not had the pleasure of meeting Mrs Thatcher and therefore it could not be a mark of affection. It would appear that he concluded that the badge was a piece of red meat being dangled before his eyes.

As it happens, Romanes' sister, 'a very conscientious and accurate observer', had an even more perspicacious dog (Romanes 1882, p. 455) who displayed 'a most unmistakable recognition of portraits as representatives of persons', the evidence for which is reported fully (but, alas, inconclusively). And, just to cite one more example, earlier writers were just as

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

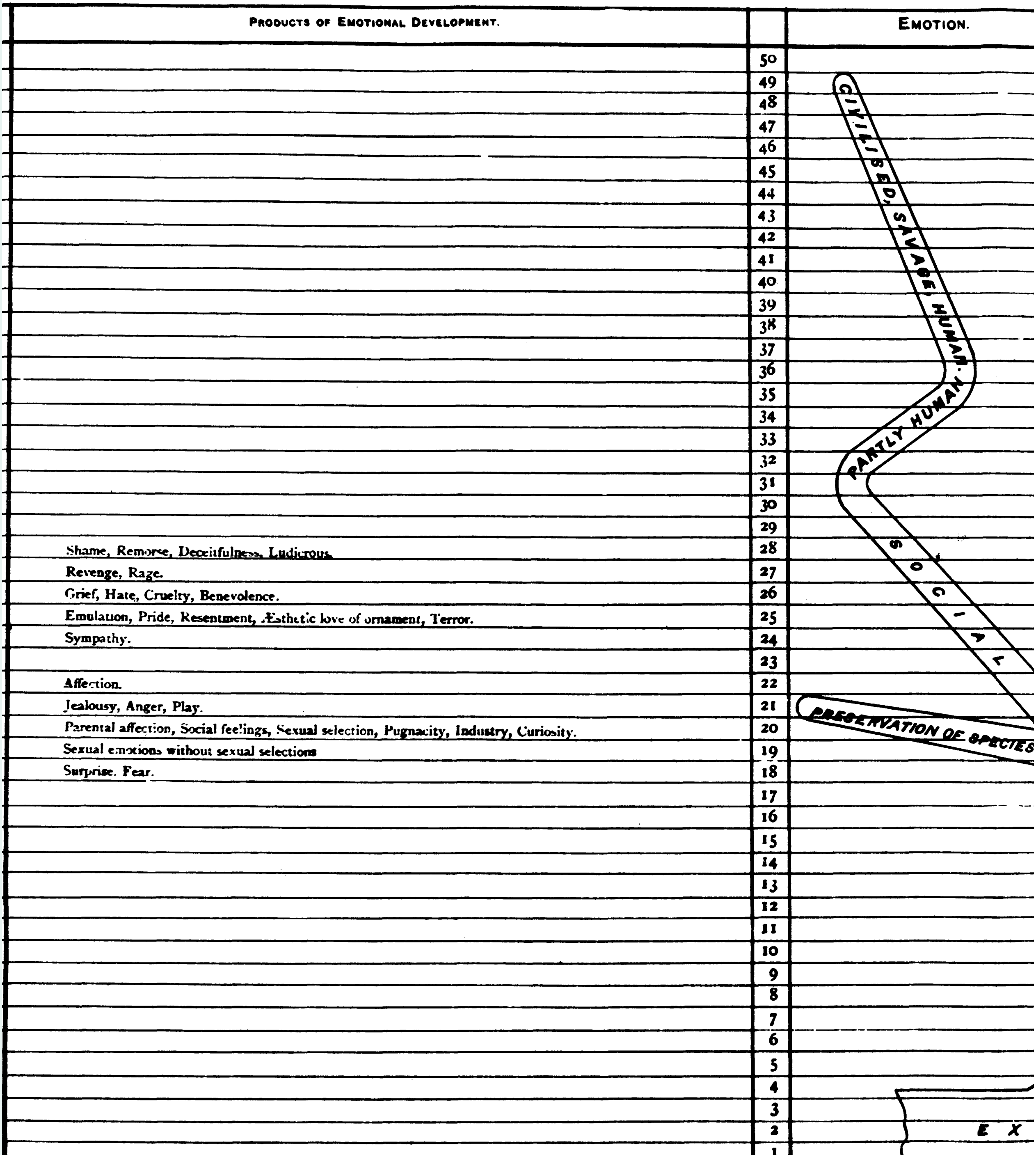
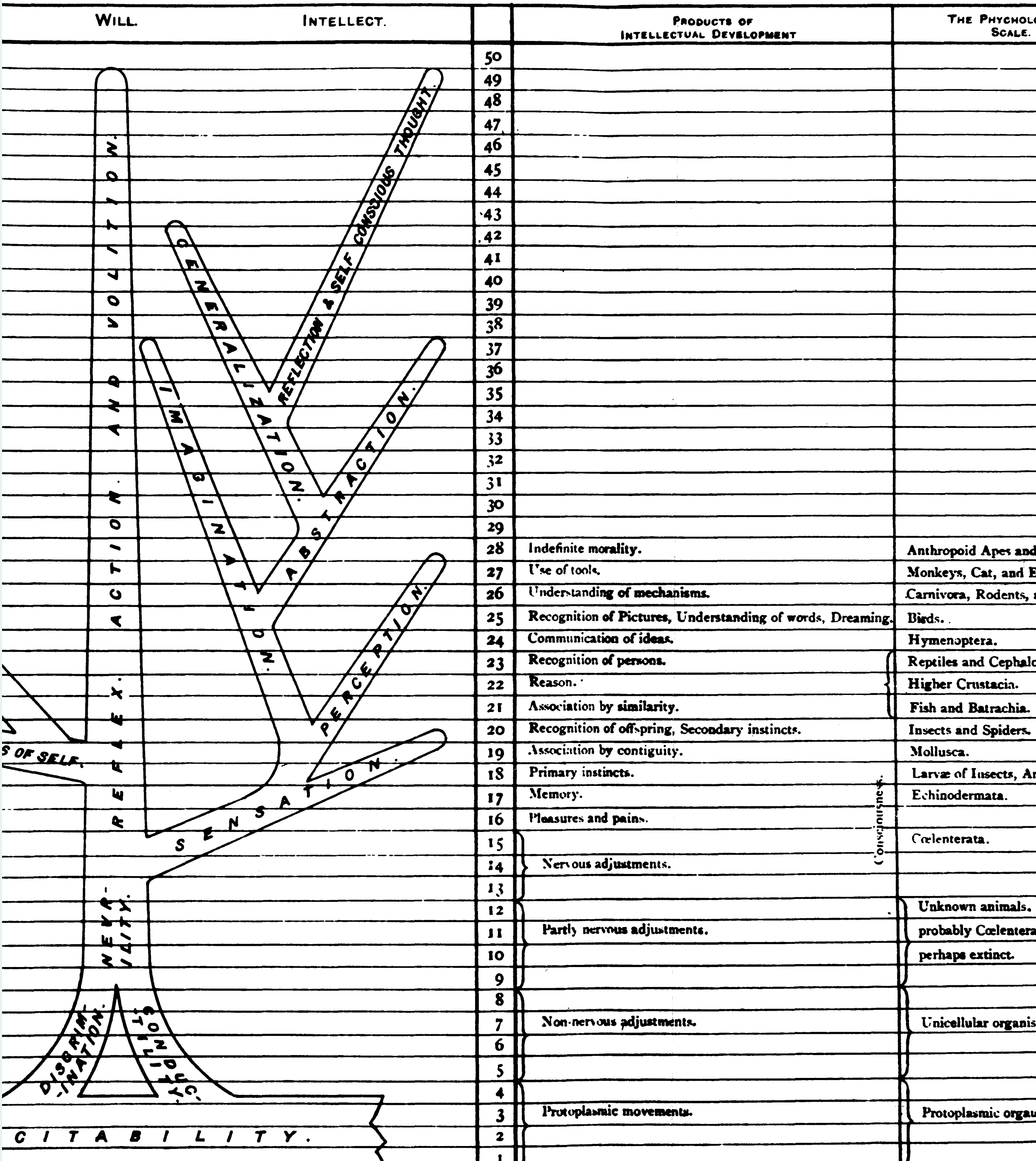


FIGURE 1. Scale of



phylogenetic intelligence proposed by Romanes (1883).

…OGICAL	PSYCOGENESIS OF MAN.	
		50
		49
		48
		47
		46
		45
		44
		43
		42
		41
		40
		39
		38
		37
		36
		35
		34
		33
		32
		31
		30
		29
… Dog.	15 months.	28
…lephant.	12 months.	27
…nd Ruminants	10 months.	26
	8 months.	25
	5 months.	24
…pods.	4 months.	23
	14 weeks.	22
	12 weeks.	21
	10 weeks.	20
	7 weeks.	19
…nelida.	3 weeks.	18
	1 week.	17
	Birth.	16
		15
		14
		13
		12
…ta.		11
	Embryo.	10
		9
		8
…ms.		7
		6
		5
		4
…isms.	Ovum and	3
		2
	Spermatozoa	1

explicit about both the possible purposes and origins of 'consciousness' as is, say, Sperry in his contemporary writings. Lloyd Morgan, whose strictures are often quoted incompletely, put the 'emergence' theory quite crisply (as well as a criticism of it), and despite his caution, introduced consciousness just as directly into the causal chain: 'consciousness is no longer merely a passenger in the ship of life. We may rather liken it to the captain of a modern ironclad, who, seated in the conning tower, directs all the movements and all the actions of the ship under his command' (1896, p. 276).

These are topics to which we shall return, but having pointed out similarities, we should turn to consider the differences between now and 1884.

First, there is no longer the concentrated concern with the comparative capacities of different species. This is not to say that there is not a strong interest, as we shall see from Professor Jerison's presentation, in correlations of cognitive capacities with encephalization, but this is a concern of the relation between cognition and the brain and its evolution, rather than with phylogenetic categories, as such. An example of a characteristically elaborate speculation of the 1880s is that of Romanes (figure 1, reproduced from original, 1883, including misspellings). But there was, even in Romanes' time, considerable disgreement about the relevance of phylogeny, although there was a splendidly direct attitude towards investigating it: Romanes (1882) freewheels through the animal kingdom in a single volume, reporting (mainly) anecdotal evidence on the emotional and intellectual powers of molluscs, ants, bees, termites, spiders, fish, reptiles, birds and mammals, with particular chapters on elephants, cats, foxes, dogs, monkey, apes and baboons. He enlisted the collaboration of his sister in making detailed observations on an allegedly tool-using monkey and the portrait-recognizing terrier. Hobhouse was much more direct: he simply went out and studied not only household pets, such as dogs and cats, but managed to do experiments himself on monkeys of several species, a chimpanzee, an elephant and an otter. He, along with Jennings (1904), would probably agree with Macphail's conclusions that there are no species differences that cannot be attributed indirectly to perception or motivation, but this point is bound to be controversial or at least tentative. Jennings took this very far: 'if *Amoeba* were a large animal, so as to come within the every-day experience of human beings, its behaviour would at once call forth the attribution to it of states of pleasure and pain, of hunger, desire, and the like, on precisely the same basis as we attribute these things to the dog' (p. 336). In the same vein, he later warns us that if *Amoeba* 'were as large as a whale, it is quite conceivable that occasions might arise when the attribution to it of the elemental states of consciousness might save the unsophisticated human being from destruction that would result from lack of such attribution' (p. 337).

Second, the main thrust of enquiry in the 50 years or so following *Origin of species* was on problem-solving. It was almost an account of how one would select animal candidates for the British civil service or the army officer corps. The extraordinary variety of problems set the great variety of animals by Hobhouse were ingenious and telling, as was Köhler's work on the Tenerife chimpanzees; they were a sort of ethology of animal cognition. Hobhouse had experiments with push-back bolts on boxes, stoppers, loops, weights, string-pulling, opening drawers, levers (including what could be called a Skinner box), door-pushing, sliding lids, pushing food out of long tubes with sticks, to mention just a few. Yerkes had an almost identical food-in-tube problem, also for chimpanzees, without acknowledgment of Hobhouse's work. Köhler's highly influential work was similarly concerned with giving animals problems to solve, and a certain amount of the work of the Tolman school, not to mention Maier's work on problem-solving in rats, falls into the same category. The current work, in contrast, is concerned rather more with trying to construct the *structure* of an animal's psychological world, as in the spatial memory work of Olton and associative learning of Gaffan, and, of course, most notably the chimpanzee work of Menzel, Savage-Rumbaugh and Rumbaugh, and Terrace. The question is not whether an animal is clever, but in which way does an animal remember and *think*.

Third, today's efforts are much more systematic and focused: perhaps not surprisingly, given the plethora of revelations over the past 100 years of how one can be misled. Rather than ranging widely over a number of species and a number of problems, today's investigators are much more focused on a particular aspect of one species' performance. Virtually every speaker at this meeting exemplifies this point, but Herrnstein's impressive work on categorization is a very good example. The ratio of empirical evidence to dogmatic assertion has increased gradually but very substantially, and there is sober recognition of just how much hard work is required to establish a fact. Fabre's dictum has gradually won out: '...a thousand theoretical views are not worth a single fact...Problems such as these, whether their scientific solution be possible or not, required an enormous mass of well-established data' (1919, p. 108). But this is, of course, relative. Hobhouse and Lloyd Morgan certainly focused much attention on the behaviour of the dog, and their descriptions, especially the former's, are exceedingly detailed and careful. Lloyd Morgan spent a great deal of time in observing the unsuccessful behaviour of a dog with a stick in its mouth when it comes to a narrow gap in a vertical grill or railing, and thought it an impossible task, even with training. 'Two of my friends criticized these results, and said that they only showed how stupid *my* dog was. *Their* dogs would have acted very differently. I suggested that the question could easily be put to the test of experiment. The behaviour of the dog was in each case – the one a very intelligent Yorkshire terrier, the other an English terrier – similar to that above described. The owner of the latter was somewhat annoyed, used forcible language, and told the dog that he could do it perfectly well if he tried' (1900, p. 143).

Fourth, the role of anecdotal evidence has changed, although one must be cautious about this: as Ghiselen remarked recently (1983), 'a respectable ethologist might call...anecdotal evidence nothing more than good observation in the field', and probably very few would agree with Seidenberg (1983) that 'behavior so novel that it can't be observed more than once can't be understood'. Many of today's anecdotes are contrived, they are experimental programmes in miniature, and even when not they are cast in the form of answering rather specific questions. This can be contrasted with the observation of Darwin's recounted in his letter to Romanes (20 August 1878, cited in Romanes 1896, p. 76), no doubt written with tongue pointing gently towards a cheek, but probably no more: 'Have you ever thought of keeping a young monkey, so as to observe its mind? At a house where we have been staying there were Sir A. and Lady Hobhouse [not, incidentally, *the* Hobhouse to whom we have been referring], not long returned from India, and she and he kept three young monkeys, and told me some curious particulars. One was that the monkey was very fond of looking through her eye-glass at objects, and moved the glass nearer and further so as to vary the focus. This struck me, as Frank's son, nearly two years old (and we think much of his intellect!) is very fond of looking through my pocket lens, and I have quite in vain endeavoured to teach him not to put the glass close down on the object, but he will always do so. Therefore I conclude that a child just under two years is inferior in intellect to a monkey.' Fabre, as usual, was scathing about such effortless comparisons: 'To disparage man and exalt animals in order to establish a point of contact, followed by a point of union, has been and still is the general tendency of the "advanced theories" in fashion in our day. Ah, how often are these "sublime theories", that morbid craze of our time, based upon "proofs" which, if subjected to the light of experiment, would lead to ... ridiculous results' (1916, p. 128).

Fifth, there is a flowering of interest in cognition as nurtured by and revealed in social interaction. While Yerkes, as a relatively modern author, had some interest in chimpanzee diads, as of course do the Gardners and the Rumbaughs, few in the past have had the focused interest in social phenomena shown today by Hans Kummer, Jane Goodall, Robert Seyfarth and Dorothy Cheney, and Emil Menzel; and Nicholas Humphrey (1983) has argued that the demands of social knowledge are a major source of pressure for mental evolution.

Sixth, the fields of human cognitive psychology and cognitive neuropsychology have themselves developed in recent years in such a way that animal workers are asking new theoretical questions that stem directly from the human studies. Terrace's work on serial learning and knowledge of ordinal position is a nice example of such a development. Similarly, much current work on animal memory can be characterized in this way, drawing especially on evidence from human neuropsychology.

Seventh, there is the striking development of interest in human sign language as either taught to animals or as considered in relation to animal gestures. There was no lack of interest in the relevance of the deaf to animal communication in the 19th century. but the main impact was to relegate the deaf to the level of brutes. Thus, Romanes in an evening discourse to the British Association (16 August 1878) remarked: '...it occurred to me that a valuable test...was to be found in the mental condition of uneducated deaf-mutes. It often happens that deaf and dumb children of poor parents are so far neglected that they are never taught finger language, or any other system of signs, whereby to converse with their fellow creatures. The consequence, of course, is that these unfortunate children grow up in a state of intellectual isolation, which is almost as complete as that of any of the lower animals.' He goes on to say he has obtained all the evidence he could about such persons who happened to become educated afterwards. 'I find that their testimony is perfectly uniform. In the absence of language, the mind is able to think in the logic of feelings, but can never rise to any ideas of higher abstraction than those which the logic of feelings supplies. The uneducated deaf-mutes have the same notions of right and wrong, cause and effect, and so on, as we have already seen that animals and idiots possess. They always think in the most concrete forms, as shown by their telling us when educated that so long as they were uneducated they always thought in pictures. Moreover, that they cannot attain to ideas of even the lowest degree of abstraction, is shown by the fact that in no one instance have I been able to find evidence of a deaf-mute who, prior to education, had evolved for himself any form of supernaturalism.' He concludes, 'on the whole, then, from the mental condition of the uneducated deaf-mutes we learn the important lesson that, in the absence of language, the mind of man is almost on a level with the mind of a brute in respect of its power of forming abstract ideas'. What an extraordinary number of issues are compressed into this short extract!

Darwin was, of course, deeply interested not only in natural gestures and their role in communication, remarking that 'any one who has watched monkeys will not doubt that they perfectly understand each other's gestures and expression, and to a large extent, as Rengger asserts, those of man' (Darwin 1872, p. 60), but also in 'conventional signs which are not innate, such as those used by the deaf and dumb and by savages', with particular interest in the 'principle of opposition' within the sign language of, for example, the Cistercian monks (Darwin 1872, pp. 60–61). But the entire emphasis in Darwin is upon phylogenetic continuity: 'every true or inherited movement of expression seems to have had some natural and independent origin' (p. 355), and he would have welcomed Terrace's pertinent question as to 'how alarm calls of vervet monkeys differ from bird calls or from other familiar examples of animal communication. In each case there is a "vocabulary" of communicative acts' (Terrace 1983, p. 378). Darwin himself quotes an account that the *Cebus azaroe* in Paraguay utters at least six distinct sounds, and 'monkeys...when wild, utter signal-cries to their fellows; and...fowls give distinct warnings for danger on the ground, or in the sky from hawks (both, as well as a third cry, intelligible to dogs)' (Darwin 1871, p. 87). But Darwin's and his contemporaries' interest never extended, as far as I can discover, to the possibility of teaching such a system to 'brutes', which was the seminal contribution of the Gardners, nor to any deep effort to probe the linguistic properties of sign language or artificial 'token' languages.

Finally, today's work is set against a lengthy background of theories and systems of animal learning and memory that started with Pavlov and Thorndike, but has been richly, if contentiously, ramified in the work and theoretical structures of Tolman, Harlow, and many modern workers, as represented in our meeting by Mackintosh and Dickinson. Similarly, field work has flourished along with the fruitful developments in ethology, which have lent a sophistication to methods of observing animals plus a fertile background of knowledge concerning the daily habits of a variety of creatures in this field, as is evident in the contributions of Jane Goodall and Hans Kummer. And so this conference is one where these two major strands – careful field work plus the logical dissection of laboratory work – have an opportunity to converge.

2. Some illustrative current work in context

I want now to turn to some illustrative points that emerge from the work of some colleagues and myself, starting first of all with the capacity of abstraction which Locke, an empiricist (or, what Wolfgang Köhler used to call disparagingly, an 'empirist'), decreed was a capacity that brutes did not possess: it 'puts a perfect distinction betwixt man and brutes (Locke 1690, vol. 1, p. 126). Herrnstein (this symposium) and his coworkers, Morgan *et al.* (1976) and others, have shown that pigeons are exquisitely capable of grouping pictures of things, for example, trees, fish, oak leaves, faces, letters of the alphabet, symmetrical compared with asymmetrical shapes, efficiently and quickly into classes. I was struck by a comment of Herrnstein's in a recent paper (1984): 'To categorize, which is to detect recurrences in the environment despite variations in local stimulus energies, must be so enormous an evolutionary advantage that it may well be universal among living organisms. Seen in this light, categorization is just object constancy, which is perhaps the fundamental constancy toward which all other perceptual constancies converge. Rather than psycholinguistics, it is the psychology of perception and stimulus discrimination that impinge most directly on categorization.'

For some time I have been pursuing experimentally just this fundamental constancy in monkeys. The fundamental importance of object constancy for an animal's survival in the real world of stable objects is, I believe, hard to over-estimate, and yet we know very little about the mechanisms. The world is not a buzzing confusing place even, I suspect, to a newborn animal, but the sense organs are buzzing with a continuous flow of changing inputs.

In our work we presented the animal with a stable view of a real object, which was always rewarded with food, and after the animal learned to a criterion of 90 % correct, we randomly injected probe trials in which the objects were altered in orientation, size, or texture-shadow arrangement (figures 2, 3 and 4). To teach the animal the original discrimination, the rewarded object must be contrasted with a negative object. We used new and different negative objects on every trial, so that we did not have to worry about making equivalent transformations for both negative and positive stimuli. The details are described in Weiskrantz & Saunders (1984).

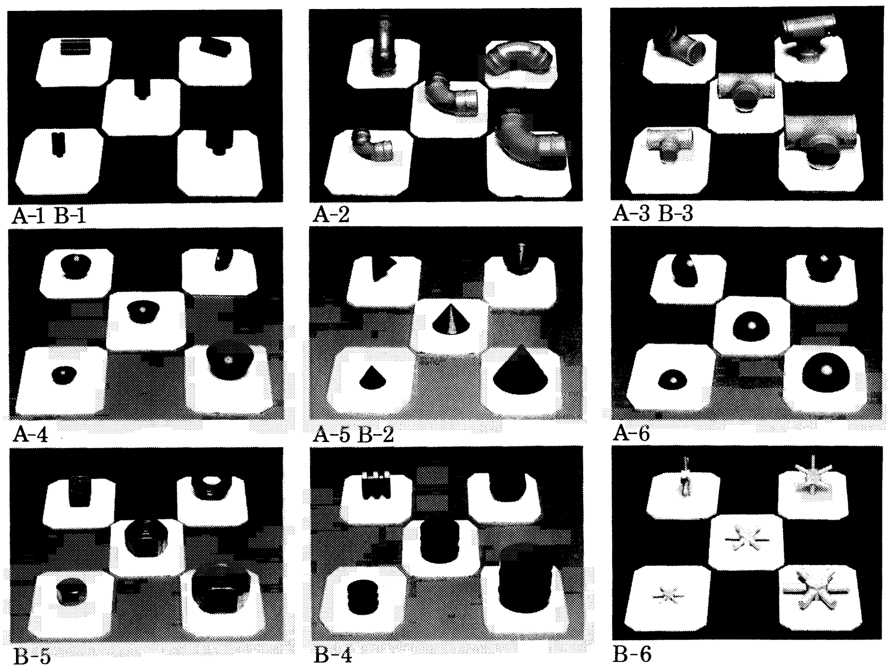
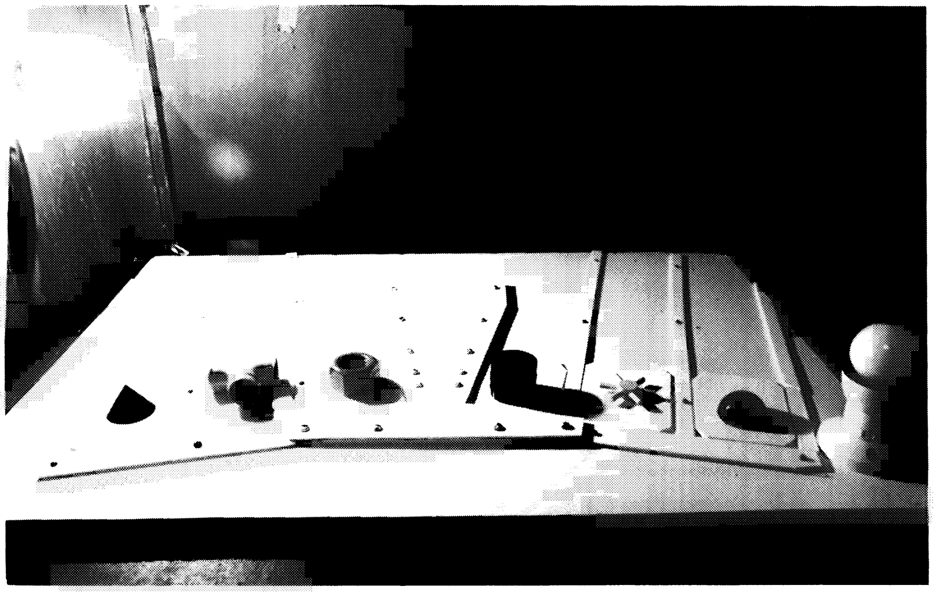


FIGURE 2. Photographs of stimulus objects with size and orientation transforms. View of object in the centre of each panel is of standard training object. The forward views are of the two size transforms, and the back views are of the two orientation transforms. Each white base plaque is 7.5 cm wide. (Reproduced by permission from Weiskrantz & Saunders (1984).)

On the very first problem in which naive animals were given their very first choice with transforms of the original object, they performed at well above chance on all three types of transforms, even though our training method would have biased them towards rejecting them (because the animals always failed to obtain reward for choosing novel objects). If we group together the first transform trials of the six problems used per animal in the study, a naive group performed at about 80 % correct (chance being 33.33 %). With more test sophistication, performance can become very efficient indeed. Our best group made only about 6 %, 10 % and 2 % errors on the first occasions on which they saw shadow, orientation, and size transforms (out of 48 trials per transform type). It must be stressed that we can be sure that these transforms had never been seen before by the animals in their entire lives, and therefore they necessarily stimulated a fresh grouping of, for example, 'orientation' neurons in the striate cortex. And yet each virgin image was able to address the canonical or prototypical store with impressive efficiency. We have also tried to discover whether some regions of the brain are critical for this capacity, and it appears that the neocortex of the temporal lobe plays an especially important

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



FIGURES 3 AND 4. Photographs of the two shadow transforms, shown in a six-choice testing apparatus. (Reproduced with permission from Weiskrantz & Saunders (1984).)

role (figure 5). Our rough scheme of the organization in the monkey is shown in figure 6. We also know from the work of Warrington and her coworkers (cf. Warrington 1982), which originally inspired our own study, that patients with right posterior hemisphere lesions can be severely impaired in identifying transforms ('unusual views') of familiar objects, without suffering from any difficulty in identifying the prototypical view or any loss in acuity or, apparently, any other sensory capacities.

No one knows how widespread the capacity is in the animal world: do crabs have it? Köhler (1915) made observations suggesting that young hens have it as regards shadow transforms. Marr (1982) has speculated on the computational aspects of the problem, but no one knows

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

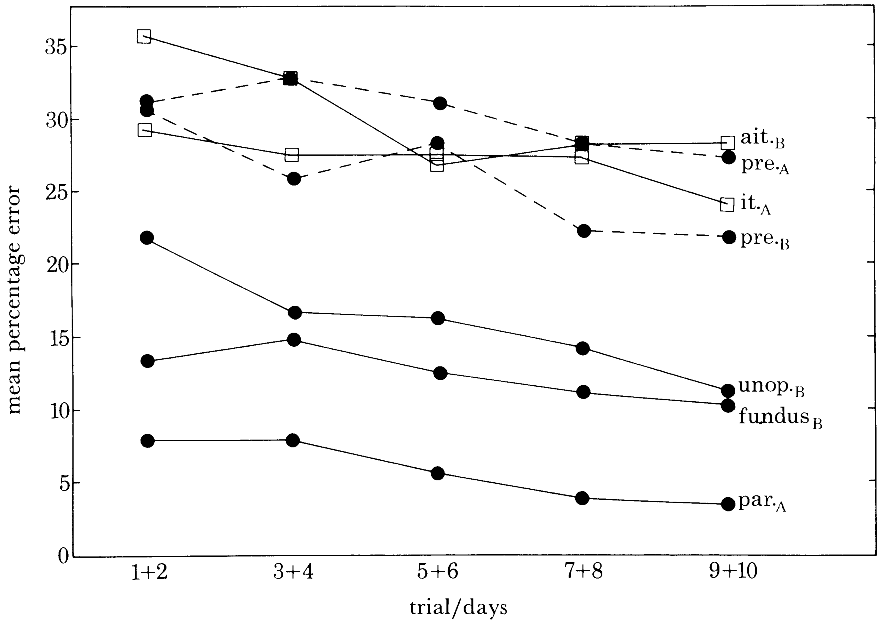


FIGURE 5. Mean percentage errors on transforms as a function of trials within all problems for each group of monkeys. Top three groups had lesions in various regions of inferotemporal neocortex: bottom three groups were controls. (Details in Weiskrantz & Saunders (1984).)

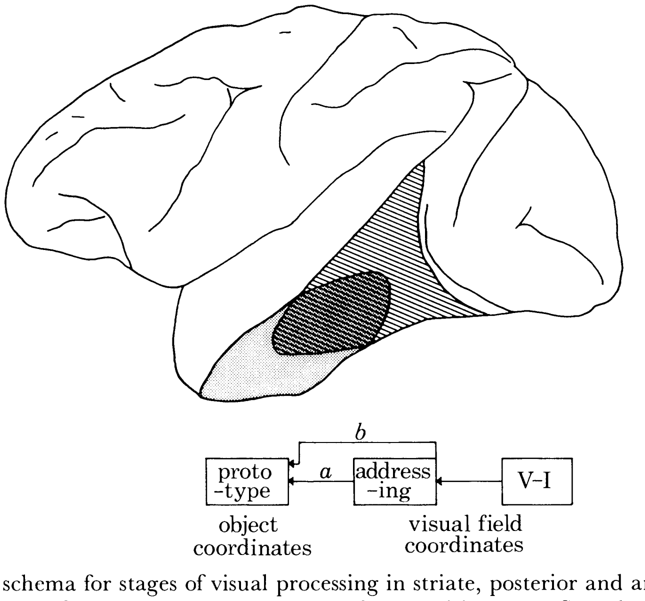


FIGURE 6. Hypothetical schema for stages of visual processing in striate, posterior and anterior inferotemporal cortical regions. (Reproduced with permission from Weiskrantz & Saunders (1984).)

in detail how the brain actually generates a stable representation of an object, with a coordinate system of its own, out of coordinates that are 'glued' to the animal's own retina. This is not the place to speculate, but merely to comment that it is an act of possibly universal but automatic intelligence. The achievement is clever, more clever than any machine has yet achieved, and is a prerequisite, perhaps even the foundation, for all visual abstraction and categorization, which is the attachment of identity of a thing with itself or of groups of things together. 'If a being has the power of thinking "thing" or "something", it has the power of transcending space and time.... Here is the point where intelligence ends and reason begins.' So Lloyd Morgan quotes Mivart with enthusiastic approval (1890, p. 375).

But such cleverness is unthinking, what Lloyd Morgan would call 'practical' intelligence. 'I wish [in no way] to disparage intelligence. Nine-tenths at least of the actions of average men are intelligent and not rational. Do we not all know hundreds of practical men who are in the highest degree intelligent, but in whom the rational, analytical faculty is but little developed? Is it any injustice to the brutes to contend that their inferences are of the same order as those of these excellent practical folk?' Trying to make amends to his brutes, he adds, 'if I deny them self-consciousness and reason, I grant to the higher animals intelligent inferences of wonderful accuracy and precision... in some cases, no doubt more perfect even than those of man, who is often distracted by many thoughts' (1890, p. 377). Hobhouse, similarly, concluded after the massive survey of his own experiments, 'none of my animals (with the possible exception now and again of the monkeys) showed the least understanding of the how or why of their actions, as distinct from the crude fact that to do such and such a thing produced the result they required.... What Jack (his dog) or the elephant knew was, crudely that they had to push [a] bolt.... The reason why... they obviously never grasped' (1901, p. 235).

Elsewhere Lloyd Morgan (1900, p. 59) makes a distinction that follows on from our own progression: he talks of a simpler level as belonging to the 'perceptual stage' and of a higher 'ideational' stage (following Stout) which embraces reflective thought, requiring 'deliberate attention to the relationships which hold good among the several elements of successive situations'.

Psychologists, from Köhler onwards, have in fact struggled with the question of reflective thought in animals, in just this sense of examining an animal's 'attention to the relationships which hold good among the several elements'. They tried, with some ingenuity and persistence, to put the matter under direct observation in controlled quasi-laboratory situations, within broadly defined theoretical frameworks, such as Tolman's. Perhaps the person who concentrated most strongly upon the problem was N. R. F. Maier (1929), who studied 'reasoning' in rats, by which he meant seeing whether an animal given experience of different spatial layouts could put them together to solve a new spatial problem. One of the difficulties in the work, which was heroic in scope, was in defining the individual 'elements', which were complex, and also, as in Köhler's work, the animal's past experience, which Harlow showed to be of such central importance in transforming slow learning into 'insightful' learning.

We have recently explored a different approach to the same problem, starting with observations from the neurological clinic. There are patients, about whom I shall say more later, who are unable to learn lists of paired-associate words. This is a task that is known to be heavily influenced by the capacity to link two supposedly unrelated words together by images in thought. Saunders and I have tried to see whether we could teach an animal a paired-associate task, not of words of course, but of visual objects. The strategy was to train the animal in stages on the following task, where each letter stands for a particular object and each + means food reward and each − means no food reward. (The details are in Saunders (1983).)

$$\overset{+}{A}\,\overset{+}{B} \text{ versus } \overset{-}{A}\,\overset{-}{C} \qquad\qquad \overset{-}{D}\,\overset{-}{B} \text{ versus } \overset{+}{D}\,\overset{+}{C}$$

$$\overset{+}{A}\,\overset{+}{B} \text{ versus } \overset{-}{D}\,\overset{-}{B} \qquad\qquad \overset{+}{D}\,\overset{+}{C} \text{ versus } \overset{-}{A}\,\overset{-}{C}$$

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

It will be noted that each object is equally often rewarded and non-rewarded, depending on its partner. If we examine the top two discriminations, it will be noted that B is positive and C is negative when paired with A, and just the reverse when each of these is paired with D. In the final stage, we presented one of the objects in isolation, and asked the animal, in effect, to 'think': what had it gone with when rewarded? If A, then B was the correct object, and not C. If D, then C and not B.

$$\begin{array}{cccc} \overset{+}{\mathrm{B}} & \overset{-}{\mathrm{C}} & \overset{-}{\mathrm{B}} & \overset{+}{\mathrm{C}} \\ & & & \\ \multicolumn{2}{c}{\overset{+}{\mathrm{A}}} & \multicolumn{2}{c}{\overset{+}{\mathrm{D}}} \end{array}$$

We found positive evidence that monkeys could do this, our control being the presentation of the last stage without experience of the previous pairings. Most interestingly, with lesions meant to simulate some of the same features as seen in patients, the crucial group of animals had no difficulty in learning the original task, but were impaired in the final stage. And so learning that an object or a pair of objects inevitably leads to food is not sufficient to enable the animal to reflect on which element went with which element.

Other varieties of stimulus–stimulus association tasks will be discussed by Gaffan. And Passingham and Dickinson, in different ways, both address the same type of issue relevant to this issue: what is the difference, theoretically and experimentally, between a task, on the one hand, that has become habitual, automatic, 'reflexive', and in which the information at hand leads directly to the acquired behavioural act (even if that task initially was complex and demanding, for example driving a car) and, on the other hand, a 'reflective' task in which the animal is able to make a fresh appraisal or reappraisal of its stored knowledge. The study of brain disorders appears to make some such distinction very important (cf. Weiskrantz 1982).

The neurological clinic also provides observations relevant to that most enduring of questions: consciousness. Like sin or poverty, the problem of consciousness will not go away, despite strenuous efforts to exorcise it. Many tried to argue that it is just an epiphenomenon, what T. H. Huxley (quoted by Lloyd Morgan) dismissed as 'simply a collateral product...as completely without any power...as the steam-whistle which accompanies the work of a locomotive engine is without influence on its machinery'. Even Lloyd Morgan could not stomach Huxley's 'steam-whistle' analogy, and replied: 'It is nothing less than pure assumption to say that the consciousness, which is admitted to be present, has practically no effect whatever upon the behaviour. And we must ask any evolutionist who accepts this conclusion, how he accounts on evolutionary grounds for the existence of a useless adjunct to neural processes' (1900, pp. 308). That the history of its conceptual status is tangled and fraught is beyond dispute, and the supposed criteria for recognizing it vary from 'learning' (Romanes), capacity for choice (Lloyd Morgan), to, among other things, 'the possession of ethical values' (Hubbard 1975). William James stressed purposive behaviour as the essential criterion: 'the pursuance of future ends and the choice of means for their attainment' (1890, p. 8), a definition that allowed him readily to endorse the view of some of his contemporary physiologists that the spinal cord of the frog displays 'conscious intelligence'. The criteria, it is clear, are as varied as the properties of adaptive behaviour themselves, and less amenable to enquiry. Here I wish to concentrate on one aspect of the problem: acknowledged awareness, the capacity to know what one is doing.

Perhaps we might acknowledge that much of the time we are unaware of our moment-to-moment activities: we can drive a car, walk down the street, wave our hands as we speak, or indeed even hold conversations about the weather, in states that are little better than sleep-walking. Of some of our responses, for example, pupillary adjustment, we are never aware. It is fortunate that we do not waste time on reflecting on such activities, or else there would be little capacity left for those activities, simultaneously present, that really do benefit from our reflection. The striking feature from neurology is that damage to certain regions of the brain prevents patients from having knowledge even of those processes for which we normally do acknowledge an awareness.

For example, patients have been reported with damage to the striate cortex who, at a very high level of proficiency, can locate visual targets in space, detect their onset, discriminate between gratings of different orientations, between moving and stationary stimuli, and yet do not acknowledge 'seeing'; they report they are merely guessing, a phenomenon that has been called 'blindsight' (Weiskrantz *et al.* 1974). The precise neurological status of 'blindsight' is a matter of controversy (cf. Campion *et al.* 1983) but not the reported phenomena themselves. The problem is not one merely of verbal disconnection, as in split-brain patients, because the discriminative response can be either verbal or non-verbal. And in this sense, the blindsight patients behave differently, in my experience, from those split-brain patients of Sperry's whom I have seen (but who also demonstrate, of course, another form of a clear dissociation between skilled discriminative capacity and acknowledgement of awareness (Sperry 1974). The problem for the blindsight patient is not whether he speaks or not but the type of question he is trying to answer and the type of decision he makes: it is the distinction between *reacting*, which he can do, and *monitoring*, which he is apparently unable to do, or is at least very deficient in doing.

Perhaps even more striking are those patients who can be shown to be capable of learning and retention, but who have no acknowledged 'memories' associated with doing so, the so-called amnesic syndrome patients. So ineffective are their own acknowledgements that for a long time the patients were thought actually to have lost the ability to learn anything new at all. But it is now clear from the work of many workers that these seriously disadvantaged patients can, for example, learn new motor skills, can show verbal and perceptual learning, can acquire conditioned reflexes and many other tasks, and yet show no recognition of the situations in which these tasks were presented or that their own performance has changed as a result of prior exposure. For example, a patient can acquire a conditioned eyelid response (figure 7), and yet be unaware of the (to us) highly memorable set of events. Nevertheless, he will respond appropriately to the light and tone that precede the puff of air to the eye, showing clear evidence of conditioning. When questioned (sitting in front of the apparatus) in the frequent brief rest pauses, he would simply invent accounts about what was going on: for example, that his knowledge of languages was being tested (Weiskrantz & Warrington 1979). We have argued (Warrington & Weiskrantz 1982) that the amnesic patient can learn and retain events that are reliably predictable, where there is redundancy and hence the possibility of automaticity either of forming habits, or of simply strengthening an item through sheer exposure, as in so-called 'priming' tasks. Inconsistency from occasion to occasion, as in a recognition situation with repeated stimuli, is apt to require reflection, matching, ordering, and reordering; what the amnesic patient is unable to do is manipulate his own memories 'in thought'. Indeed, for all of us it would seem that automatic memories are devoid of any awareness of being memories as such: we do not attach such a quality to our everyday words, although these obviously have

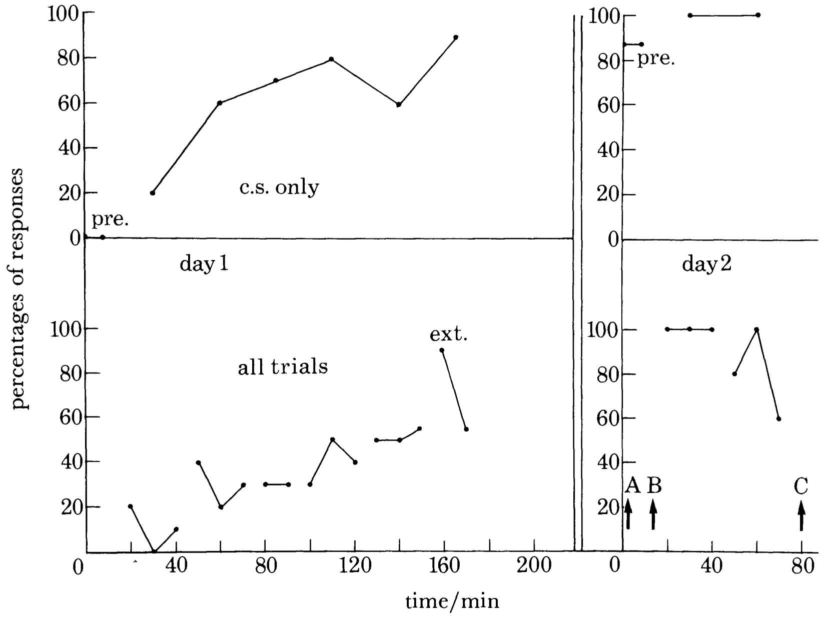


FIGURE 7. Percentage of conditioned eyelid responses for one amnesic subject. Top panel shows 'probe' trials in which the conditioned stimulus (c.s.) was delivered without the unconditioned stimulus on a random schedule. Bottom panel shows conditioning and all other trials combined. Interruptions in graph indicate occurrence of 10 min rest breaks in which subject was interviewed. (Reproduced with permission from Weiskrantz & Warrington (1979).)

been learned. We do not attach such a quality to seeing a traffic light: we stop without reflecting that we 'remember': red means stop. If we do reflect, we are apt to stop for more catastrophic reasons! The neurological cases are useful and striking in showing how complete can be the integrity of skills of perception and learning in the face of a dissociation between them and the patient's own knowledge.

We now know that both instrumental and classical conditioning can occur at a subcortical level in the absence of cerebral cortex in mammals, provided that the stimuli are not so highly patterned as to required cortical processing (Oakley 1981; Oakley & Russell 1977). The implication that I draw from this, together with the human neurological evidence, is that 'awareness' of our behaviour is a precious commodity reserved for rather special occasions when we wish to compare one visual image with another or one piece of stored information with another, that is, to imagine and to reflect, and so there is a link between our earlier concern with reflection and our present one with awareness. It would be a waste of cerebral processing to have to continue to dwell on redundant information or automatic control.

Now, if we grant such an argument, how would we know whether an animal is aware? It is by no means a trivial question, either philosophically or practically in these days of heightened sensitivity about animal suffering. Awareness in the animal kingdom has been treated as either equivalent to being responsive, which clearly will not do, as we have seen, or as a gradually emergent property of evolving systems. The former was perhaps Jennings' view, and was Lloyd Morgan's early view: 'Suppose...a young bird seizes a bee and proceeds to swallow it, but is stung in the process; ...every step of the process is taken in the field of his conscious experience...every bit of experience, no matter how trivial...exists as such for consciousness' (1896, p. 273). The emergence view has been championed by Sperry (1970), who is, however, not very explicit in telling us how we would recognize when emergence has been achieved. The approach, in practical terms, that seems to me to be the most direct and promising is that ingeniously initiated by Beninger *et al.* (1974), who gave rats the opportunity to indicate whether they discriminate their own acts. They allowed them to face-wash, or rear up, or walk, or remain immobile as they wished, but food reward was contingent on the animals pressing a different lever in association with each of these acts. Morgan & Nicholas (1979) have followed this up in an interesting study in which they argue that one of the reasons why it is difficult actually to train a rat to do certain things, like scratch, is that such acts cannot serve as 'an adequate discriminative stimulus', which in colloquial terms means that animals may not be aware of what they are doing. I suspect that it is equally difficult to train a dog to wag its tail for food reward.

The essential step in any such analysis lies in providing the animal or the person with a parallel 'commentary' response. Not only must he be able to discriminate between A and B by pressing one or another panel, say, but he needs a third key to comment upon what he is doing on the first two keys, to give a 'yes–no' commentary on whether the discrimination was 'guessing' or not, or better still, to give a confidence rating. In everyday discourse the commentary system for ourselves is verbal, but the principle is the same whether or not we actually use words. The evolutionary value of the third key capacity is not merely to enable raw sentience to occur, but to endow us with the capacity to *compare*, to put our intercourse with the world in the form of cognitively manipulable percepts and memories: in short, to enable us to think.

We do not know at what level of neural organization in evolution the third key would start to be effective, but the essential minimal organization to be sought would be one that could fulfil a monitoring function: it cannot be a mere 'emergent' property of complexity or cleverness as such. As Sperry has argued, 'it is not merely complexity or high order organization that...endows a neural event with conscious awareness. It is rather the specific operational design of the cerebral mechanism for the particular conscious function involved. The neural mechanisms for conscious experience are not just more complex, they are specifically structured on an operational, functional basis to create particular sensations, percepts, and feelings, and to provide a rapid representation of external reality' (1970, p. 589). We do not know now just how to recognize these neural mechanisms, but I believe, somewhat optimistically, that a Discussion Meeting held in 2084 will have something to contribute to the question. Meanwhile, our meeting in 1984 will no doubt illuminate lots of other issues in ways that would have fascinated and deeply impressed our forebears of 100 years ago.

References

Beninger, R. J., Kendall, S. B. & Vanderwolf, C. H. 1974 The ability of rats to discriminate their own behaviours. *Canad. J. Psychol.* **28**, 79–91.

Campion, J., Latto, R. & Smith, Y. M. 1983 Is blindsight an effect of scattered light, spared cortex, and near-threshold vision? *Behav. Brain Sci.* **6**, 423–486.

Darwin, C. 1859 *The origin of species*. London: Oxford University Press. (Page citations from 6th edn, 1951.)

Darwin, C. 1871 *The descent of Man*. London: John Murray. (Page citations from 1894 edn.)

Darwin, C. 1872 *The expression of the emotions in Man and animals*. Chicago: University of Chicago Press. (Page citations from 1965 edn.)

Dennett, D. C. 1983 Intentional systems in cognitive ethology: the 'Panglossian paradigm' defended. *Behav. Brain Sci.* **6**, 343–390.

Fabre, J. H. 1916 *The hunting wasps*. Translated by A. T. de Mattos. London: Hodder and Stoughton.

Fabre, J. H. 1919 *The mason wasps*. Translated by A. T. de Mattos. London: Hodder and Stoughton.
Ghiselin, M. T. 1983 Lloyd Morgan's canon in evolutionary context. *Behav. Brain Sci.* **6**, 362–363.
Gruber, H. E. 1974 *Darwin on Man*. London: Wildwood House.
Herrnstein, R. J. 1894 Objects, categories, and discriminative stimuli. In *Animal cognition* (ed. H. C. Roitblat, T. G. Bever and H. S. Terrace). Hillsdale, New Jersey: Erlbaum.
Hobhouse, L. T. 1901 *Mind in evolution*. London: Macmillan. (Page citations from 1926 edn.)
Hubbard, J. I. 1975 *Biological basis of mental activity*. Reading, Massachusetts: Addison-Wesley.
Humphrey, N. 1983 *Consciousness regained*. Oxford: Oxford University Press.
James, W. 1890 *The principles of psychology*. London: Macmillan. (Page citations from 1901 edn.)
Jennings, H. S. 1904 *Behavior of the lower organisms*. Bloomington: Indiana University Press. (Page citations from 1962 edn.)
Koehler, O. 1951 The ability of birds to 'count'. *Bull Anim. Behav.* **9**, 41–45.
Köhler, W. 1915 Optische Unterssuchungen am Schimpansen und am Haushuhn. *Abh. preus. Akad. Wiss.* (*phys.-math.*) **3**, 1–70.
Locke, J. 1690 *An essay concerning human understanding*. London: J. M. Dent & Sons, Everyman's Library. (Page citations from 1961 edn.)
Maier, N. R. F. 1929 Reasoning in white rats. *Comp. Psychol. Monogr.* **6**, no. 29, 1–93.
Marr, D. 1982 *Vision*. San Francisco: W. H. Freeman and Co.
Morgan, C. Lloyd 1890 *Animal life and intelligence*. London: Edward Arnold.
Morgan, C. Lloyd 1896 *Habit and instinct*. London: Edward Arnold.
Morgan, C. Lloyd 1900 *Animal behaviour*. London: Edward Arnold.
Morgan, M. J., Fitch, M. D., Holman, J. G. & Lea, S. E. G. 1976 Pigeons learn the concept of an 'A'. *Perception* **5**, 57–66.
Morgan, M. J. & Nicholas, D. J. 1979 Discrimination between reinforced action patterns in the rat. *Learn. Motiv.* **10**, 1–27.
Oakley, D. A. 1981 Performance of decorticated rats in a two-choice visual discrimination apparatus. *Behav. Brain Res.* **3**, 55–69.
Oakley, D. A. & Russell, I. S. 1977 Subcortical storage of Pavlovian conditioning in the rabbit. *Phys. Behav.* **18**, 931–937.
Pavlov, I. P. 1928 *Lectures on conditioned reflexes*. Translated by W. H. Gantt. New York: International.
Romanes, E. G. 1896 *The life and letters of George John Romanes*. London: Longmans, Green & Co.
Romanes, G. J. 1878 Evening discourse delivered before The British Association, Dublin. London: Taylor and Francis.
Romanes, G. J 1882 *Animal intelligence*. London: Kegan Paul, Trench & Co.
Romanes, G. J. 1883 *Mental evolution in animals*. London: Kegan Paul, Trench & Co.
Saunders, R. C. 1983 Some experiments on memory involving the fornix–mammillary system. D. Phil. thesis, University of Oxford.
Seidenberg, M. S. 1983 Steps toward an ethological science. *Behav. Brain Sci.* **6**, 377.
Sperry, R. W. 1970 An objective approach to subjective experience. *Psychol. Rev.* **77**, 585–590.
Sperry, R. W. 1974 Lateral specialization in the surgically separated hemispheres. In *The Neurosciences. Third Study Program* (ed. F. O. Schmitt & F. G. Worden), pp. 5–19. Cambridge, Massachusetts: M.I.T. Press.
Terrace, H. S. 1983 Nonhuman intentional systems. *Behav. Brain Sci.* **6**, 378–379.
Warrington, E. K. 1982 Neuropsychological studies of object recognition. *Phil. Trans. R. Soc. Lond.* B **298**, 15–33.
Warrington, E. K. & Weiskrantz, L. 1982 Amnesia: a disconnection syndrome? *Neuropsychologia* **20**, 233–248.
Weiskrantz, L. 1982 Comparative aspects of studies of amnesia. *Phil. Trans. R. Soc. Lond.* B **298**, 97–109.
Weiskrantz, L. & Saunders, R. C. 1984 Impairments of visual object transforms in monkeys. *Brain*. (In the press.)
Weiskrantz, L. & Warrington, E. K. 1979 Conditioning in amnesic patients. *Neuropsychologia* **17**, 187–194.
Weiskrantz, L., Warrington, E. K., Sanders, M. D. & Marshall, J. 1974 Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain* **97**, 709–728.
Yerkes, R. M. 1943 *Chimpanzees*. New Haven: Yale University Press.

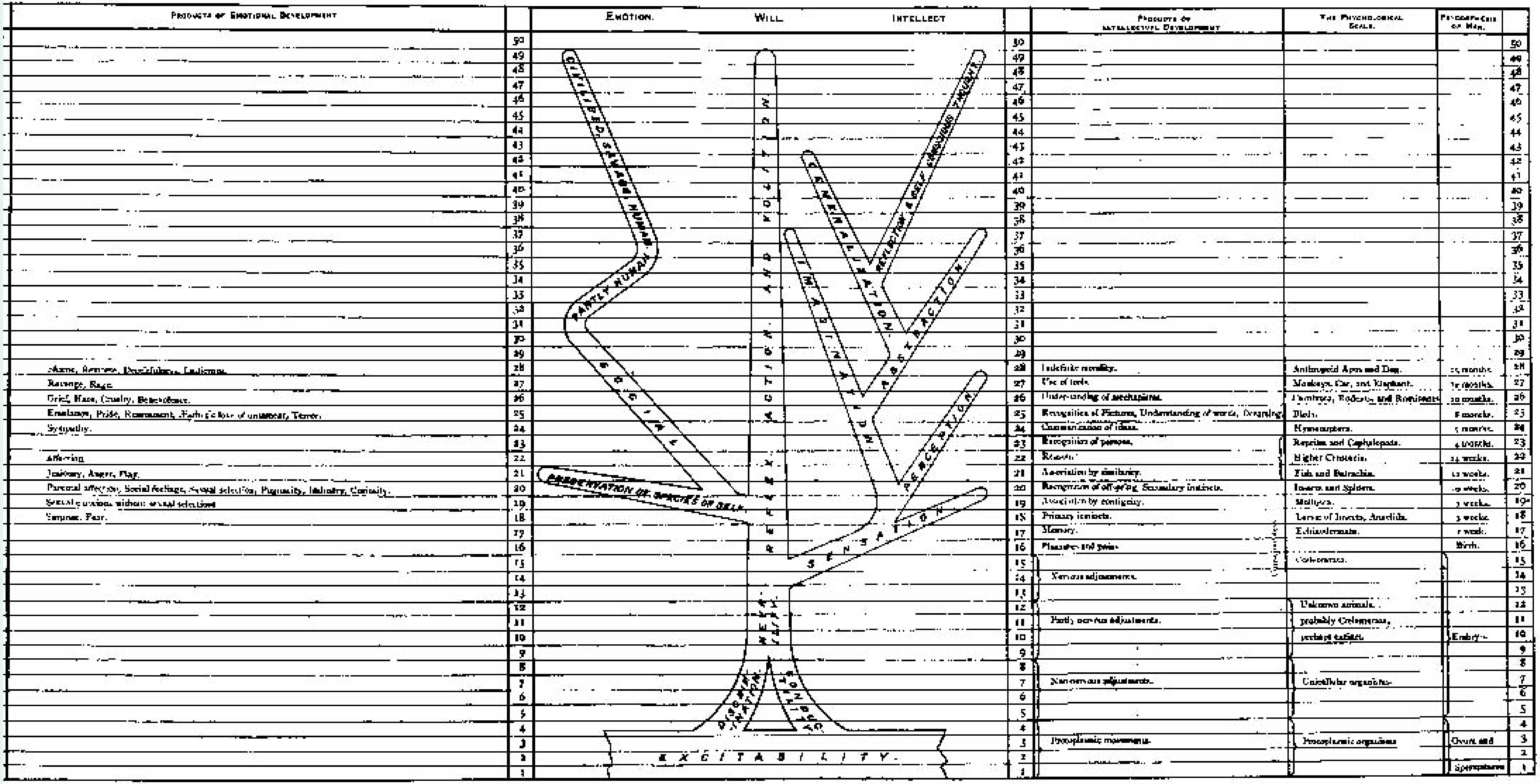


Figure 1. Scale of phylogenetic intelligence proposed by Romanes (1883).

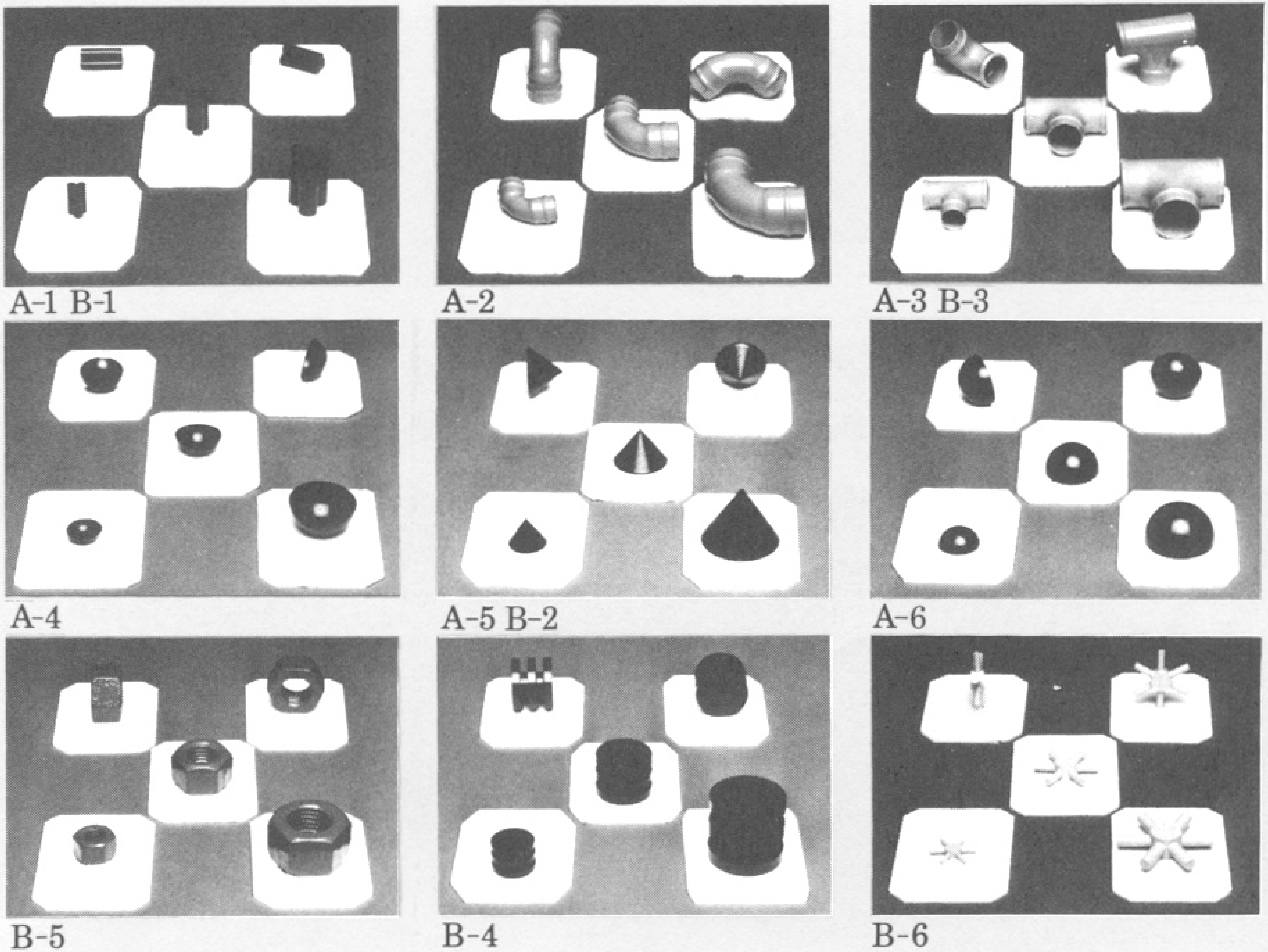
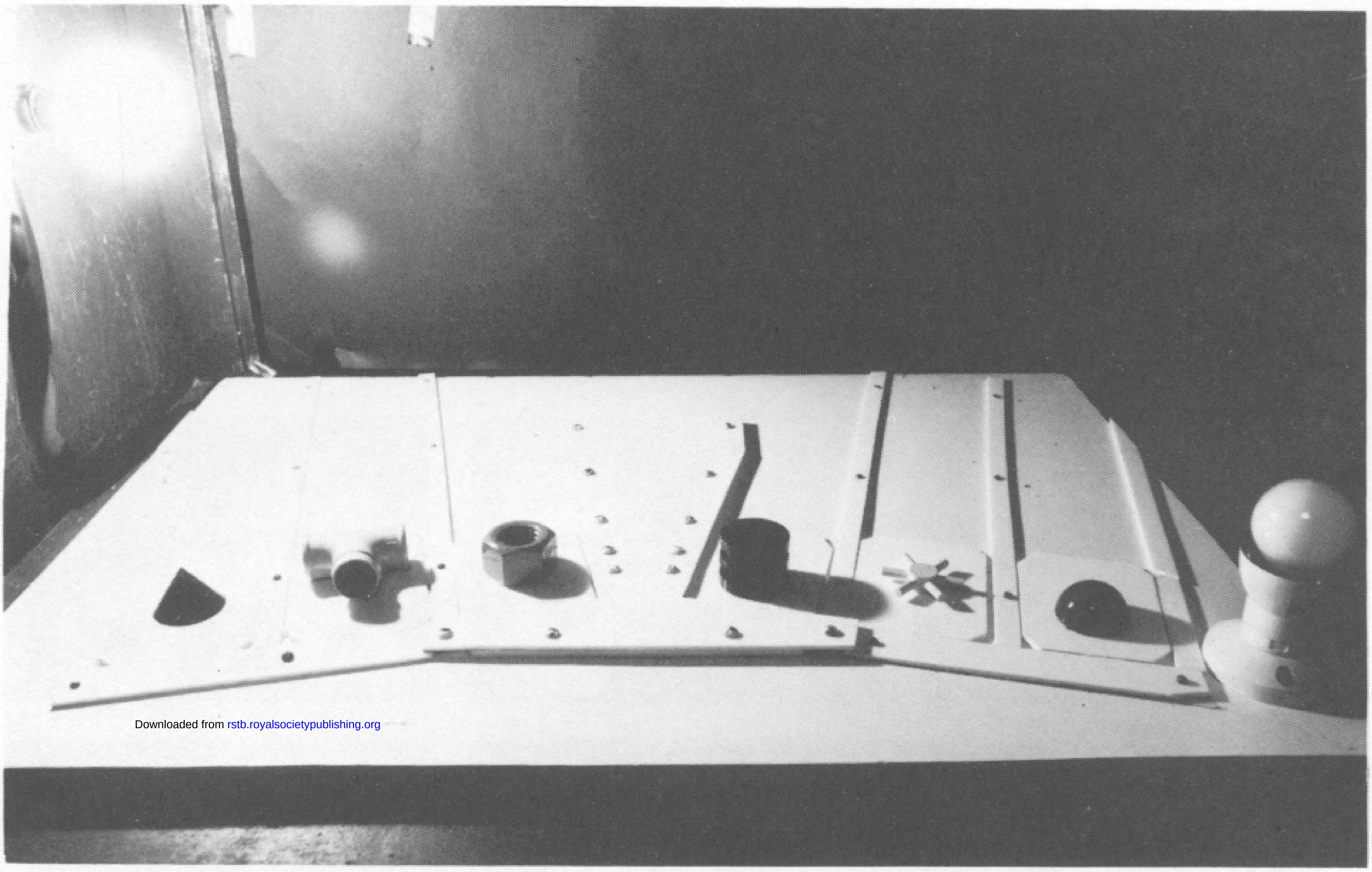
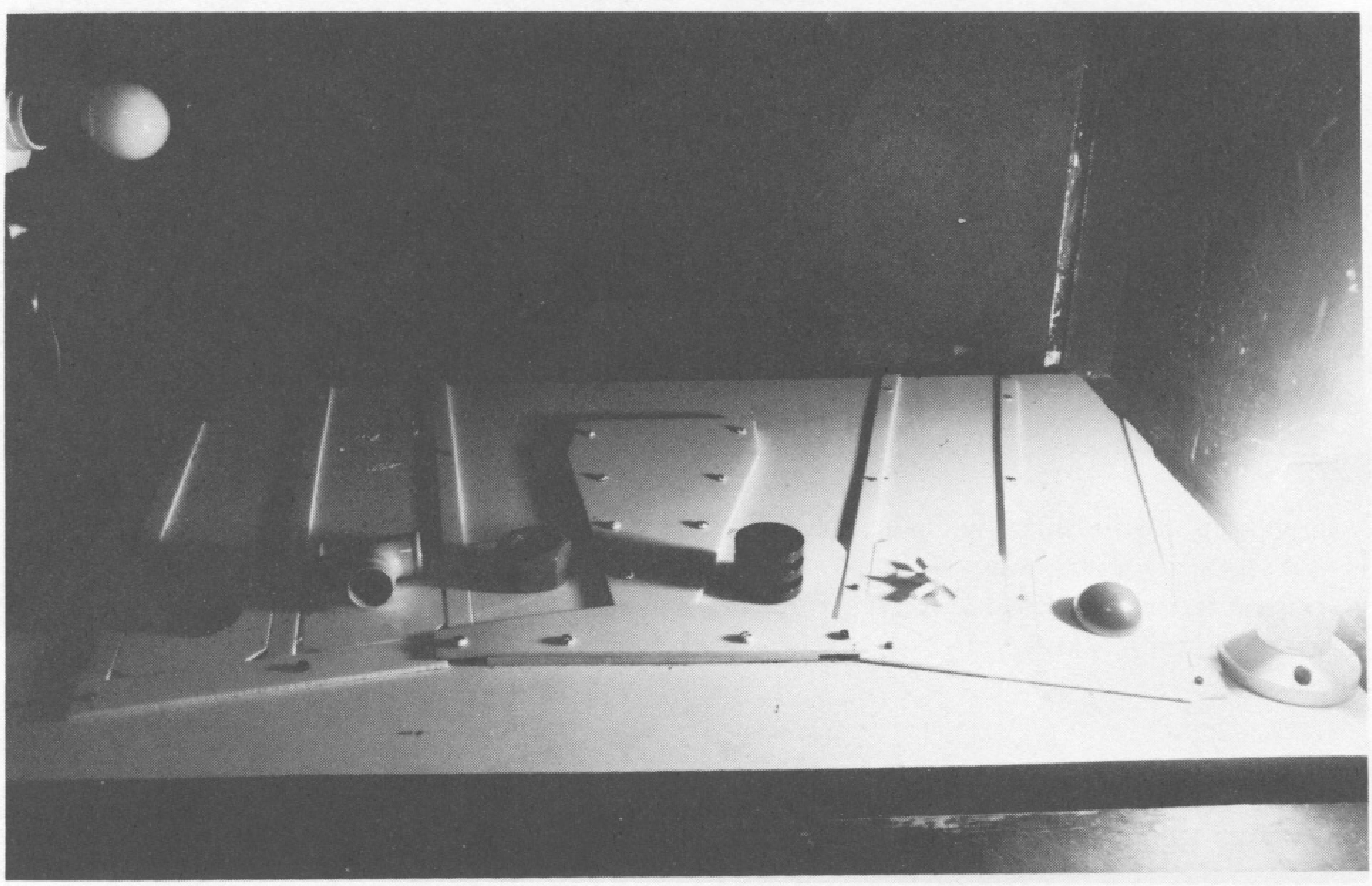


FIGURE 2. Photographs of stimulus objects with size and orientation transforms. View of object in the centre of each panel is of standard training object. The forward views are of the two size transforms, and the back views are of the two orientation transforms. Each white base plaque is 7.5 cm wide. (Reproduced by permission from Weiskrantz & Saunders (1984).)





FIGURES 3 AND 4. Photographs of the two shadow transforms, shown in a six-choice testing apparatus. (Reproduced with permission from Weiskrantz & Saunders (1984).)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES