Review article

The serial organisation of behaviour by non-human primates; an evaluation of experimental paradigms

Carlo De Lillo *

CNR, Istituto di Psicologia, Reparto di Psicologia Comparata, Via Ulisse Aldrovandi 16b, 00197 Roma, Italy

Received 17 July 1995; revised 30 January 1996; accepted 15 February 1996

Abstract

On close examination of research programs which focus, either implicitly or explicitly, on the problem of the organisation of serial order in non-human primates, it is possible to detect some limitations in the paradigms conventionally used. Serial learning studies, which focus on the acquisition of arbitrary lists of unconnected elements point towards a distinction between the representation of ordered series formed by monkeys and pigeons. However, the use of unconnected items prevents an assay of the degree to which primates might be able to impose a structure over the list to be reported. The study of transitive reasoning has been implemented by means of a paradigm where the order of a series is conveyed by presenting a common item in pairs of binary discriminations. Animals tested with this paradigm develop control strategies using more information than that provided by reward contingencies alone. A restriction of this paradigm is that, in its binary form, it does not allow a differentiation between the performance of monkeys and pigeons and even simple models account for a transitive bias in the task. On the basis of these observations it is proposed that novel paradigms which go beyond the binary context, feature multiple connected items, and accord a high degree of spontaneity to the subjects might allow better than traditional ones to uncover qualitative different ways in which different organisms serially organise their behaviour. Some recent research programs based on such rationale, and implemented as search tasks, are then outlined and compared with other approaches to the study of search behaviour. Preliminary results obtained from these studies indicate that the spontaneous serial organisation of multiple connected items might uncover new dimensions of promising comparative relevance.

Keywords: Primates; Serial learning; Serial order; Transitive inference; Search

1. Introduction

Ethologists have dedicated some attention to behaviours with evident serial components observed in natural environments such as Fixed Action Patterns (FAP) [31,61]. FAPs are reflexive or instinctive behavioural patterns with very strong genetic determinants and their sequence is by definition rigid and hardly modifiable. Therefore, although they have been useful to compare closely related species and, on the basis of small variations in similar patterns, infer something about their evolution [28], they do not seem adequate to offer a characterisation of the dimensions along which different levels of complexity can be compared in various organisms to find a path towards human intelligence [36,57].

Nevertheless, there are many contexts in which animals face the problem of having to organise long sequences of actions which are not specified on a genetic basis. To explain the acquisition of series of actions the behaviouristic tradition postulated the ubiquity of a single process, associative chaining, in all behaviours with patent serial components. The chaining theory of learning postulates that the selective reward of particular sequences of responses produces associations between temporally successive responses. Although behaviourists have proposed different versions of the chaining theory, each according a different weight to associations developed between stimuli and responses or between responses to non-adjacent items of the list, the different versions of the theory share the assumption that each response represents the discriminative stimulus for the following one.

It was Lashley [30] who pointed out that most of
serially organised behaviours cannot be explained by postulating a single mechanism to account for them. For example, from the succession of movements, which can be observed in the different gaits of a horse, such as trotting, pacing and single footing, which involves the same pattern of muscular contraction in the individual legs, but nevertheless involves a different temporal order, it can be inferred that a separate mechanism must be responsible for the serial organisation of the same atomic movements. This mechanism must work quite independently from the sensory information provided by each single movement.

On the other hand, from the misplacement errors which can occasionally be observed in behaviours which otherwise maintain their general serial structure (such as slips, interference and order mistakes which occur in speech, typewriting or music playing) it can be inferred that other forces play a role in determining the serial performance quite independently from a general motor plan of the sequence.

In extra linguistic contexts, the study of the serial organisation of behaviour has been investigated by different lines of enquiry. Each focuses on different issues and the animals are tested with different apparatuses. Nevertheless, their lowest common denominator rests in the fact that all the studies are centred on serial order, either in the behaviour of the subjects or in the form of representation which can be inferred from their behaviour. The present review provides a critical evaluation of experimental paradigms which have been used to investigate serially organised behaviours (i.e. sequences which maintain an internal order as opposed to random permutations of the serial position of their constituents) in a comparative framework. The study aims to propose new methodological approaches which might uncover psychological dimensions worth studying for their comparative relevance.

Serial learning paradigms will be considered first. Although the term serial learning could adequately be applied to competencies which underpin the performance of animals in a variety of tasks, it will be confined here to the learning of series of responses in an order arbitrarily defined by the experimenter since this is the research tradition where the term is chiefly used. The hypothetical cognitive mechanisms which have been proposed as the basis for serial learning range from associative chaining to the formation of abstract templates (often described as a spatial representation) of a series. An evaluation of these different hypotheses will be addressed together with a methodological evaluation of what the paradigm has to offer for a general characterisation of the processes underpinning the emergence of serial order in non-human species.

The second paradigm considered is the so-called five-term series task, used to investigate transitive reasoning in animals. Researchers here are interested in the mechanisms which allow the integration of information conveyed by a series of binary discriminations (the premises), connected in pairs by the presence of a common term. The cognitive mechanisms invoked to explain transitive behaviour range from the use of logic inference which integrates premises stored separately in memory, to the development of a spatial paralogical devise which condenses in a single representation all the information needed to sustain transitivity. Simple stochastic models also seem able to explain success in the task. The results will be discussed in relation to the relative economy and robustness of these different solutions and, as a methodological analysis, in relation to the appropriateness of using tasks based on binary choices to study serial competencies.

The third field reviewed will be that of search behaviour in a variety of conditions. In this review search tasks are seen as intrinsically providing rich information on the organisation of serial behaviour. As in serial learning paradigms, search allows the direct observation of serial productions. Therefore, the serial competencies of the subjects do not have to be inferred from binary contexts, as in studies on transitivity. In contrast to serial learning paradigms, however, search tasks offer the subjects the possibility of organising their behaviour on the basis of the structure of the search space without any explicit training. On the other hand, in analogy with the transitive inference task, here different solutions are warranted each allegedly involving a different level of cognitive economy. In order to keep track of the moves performed while searching, the subject can either rely on memories for each of them (a solution which poses heavy demands on the memory system) or deploy principled search trajectories which reduce the memory load.

When implemented as a spatial task, search behaviour can reveal the spatial organisation imposed by the subject on a variety of configuration of loci to explore. It has been claimed that both serial learning and transitive inference rely on the development of spatial representations and operations. The characterisation of these representations, however, has to be achieved on the basis of measures (usually reaction times) only indirectly and hypothetically related to space. By contrast, analysing the spatial trajectories of search among a set of loci we operate in a more transparent medium to detect the organising principles underlying the behaviour of the subjects.

Nevertheless, similar principles of economy and organisation can be applied to both spatial and non-spatial search tasks (such as a categorically nested set of differently coloured items, which would afford similar constraints). The conclusions of this review will be neutral as far as the details of the psychological mechanisms which underpin serial competencies in spatial and non-spatial tasks are concerned. The working hypothesis proposed here is that whatever the constituents of a
serial production, the serial organisation of behaviour poses non-trivial problems of information management for an organism which is left with merely inductive evidence for the fact that primates, if provided with memory to remember it.

The results of different studies will be interpreted as evidence for the fact that primates, if provided with enough incentive, exposure to the task, and the possibility of organising their serial productions on the basis of meaningful relationships between the units of the sequence, spontaneously exploit those constraints afforded by the situation which allow a better management of the amount of information required by the task. This might not apply to species characterised by a lower level of cognitive complexity, which by contrast rely on genetic codification of fixed sequences of actions to solve the same problem of combinatorial explosion of information. Appropriate paradigms should feature tasks which allow on the one hand the detection of those requirements which must have an high degree of generality among different taxa (because of common problems of information management) and on the other the detection of those variables which account for differences in cognitive complexity between different organisms and their possible adaptive function.

2. Serial learning

2.1. The 'forward' training procedure: chaining, chunking and representation

The main root of these studies stems from ape language projects ([47,52]; see also [34] and [64] for reviews). On the basis of an analysis of the syntactic characteristic of the 'utterances' produced by subjects of different projects, Terrace and colleagues [52,58] argued that most of the sequences of signs produced by apes could be explained as rotely learnt sequences of symbols arranged in particular orders without assuming an underlying grammatical competence. To show that such a competence was not very elaborate and might have been widespread among different zoological taxa, Terrace and his collaborators started a program to teach pigeons to perform fixed sequences of arbitrary signs. The first results showed pigeons pecking four colours in particular sequences and transferring this ability to novel arrays of colours [60,50]. This finding led to the development of an extensive program to study the competence of ordered responses in pigeons and rhesus monkeys.

The paradigm used by Terrace and his group consists in displaying (originally in an operant chamber, now on touch sensitive computer monitors) a set of items (icons of different colours or photographs of different objects). The spatial configuration of these items on the screen is varied from trial to trial to prevent the subjects from learning a chain of spatial responses. If the subject executes the sequence of responses in the order previously decided by the experimenter, a reward is dispensed. The subjects are trained by a 'forward' procedure: a single item is presented at the beginning, and then new list items are added, one at a time, until the whole sequence is learnt. Negative feedback (omission of reward and additional inter-trial interval) is provided at each point of training. For example, to teach a sequence of four items (here symbolised as ABCD), the item A is presented first, the subject responds to it and receives a reward, then the sequence AB is presented and the subject is required to touch the items in the AB order (a BA response would be penalised); once a given criterion (usually the 75%) of correct responses on the two items series is reached, the third item C is added to the sequence, and so on.

The main aim of this research program was to determine possible alternative processes underpinning serial learning when the dominant explanation of list learning was based on the chaining theory. Since according to this theory the main associations develop between successive items, the subjects should find it difficult to respond to subsets of the list which contain only non-adjacent items. However, Terrace and colleagues have shown that pigeons are able to respond accurately to pairs of non-adjacent items from an already learnt list, although they do so only if the subset contains a start and/or an end item. For example, once pigeons have learnt a five-term series ABCDE, they are able to respond accurately to the subsets AB, AC, AD, AE, BE, CE and DE, but their performance falls at chance level on the subsets BC, BD and CD. Thus, Terrace and colleagues claimed that although pigeons seem unable to form an ordered representation of the series [53,55,56], a simple chaining hypothesis fails to account for their behaviour.

An isolated attempt, within the serial learning paradigm, of providing the animals with a more structured material is a study published by Terrace [55]. Here again emerged some evidence that pigeons impose some forms of organisation upon the sequence of items to be remembered which goes beyond a simple association of successive items. Terrace [55] reported that pigeons trained with colours serving as items ABC and forms as items DE seem to 'chunk' the two classes of stimuli. In fact, an experimental group, trained with the two classes
of stimuli, learned both four-item and five-item term series much faster than control groups for which only colours were used or for which the two forms were not presented as adjacent items but interspersed among the three colours. Moreover, in subsequent test trials where non-adjacent pairs of items were presented, the experimental group performed better than the control groups. Thus, it seems that, given the opportunity, pigeons are able to decompose a sequence in two different 'chunks', a three-item one (ABC) and a two-item one (DE). Furthermore, the superimposition of such a form of organisation over the list to be remembered leads to a more accurate performance.

2.2. Spatial representation in monkeys

D'Amato and Colombo [11] pioneered the study of serial learning in monkeys (Cebus apella) and were able to demonstrate that monkeys' performance, in analogous serial learning tasks, was underpinned by processes and representations substantially different from those of pigeons.

Having trained capuchin monkeys and pigeons in an operant chamber on a five-term serial learning task, in a series of successive experiments, D'Amato and Colombo tested the subjects on a variety of tasks in which the items of the learnt series were manipulated in various ways. In one of their experiments [11], pairs of non-adjacent items were used. It was shown that, in contrast to the pigeons, monkeys were able to perform at a high level of accuracy on all of them. Furthermore, on the basis of an analysis of the latencies of the responses to each of the items of the series, D'Amato and Colombo [11] presented evidence for a linear internal representation of the series in the monkeys. The rationale of the time analysis was that if the monkeys in the course of training developed an internal linear representation of the series, one might expect to find an orderly relation between response latency to the first item of a test pair and the position of that item in the original series. For example, the response latency to the first member of a pair should increase across the test pairs AE, BE, CE, DE. The reason is that in order to decide which member of a test pair to respond to first, the subject presumably would start at the beginning of its internal representation of the series and progress through the sequence until it locates one of the displayed items. The more represented items there are to be consulted, the longer the response latency. According to this explanation the results obtained by D'Amato and Colombo [11] showed that the monkey's latency of responding to the first item of each subset of the original sequence, increased monotonically as a function of the position of the item in the original list.

D'Amato and Colombo provided further evidence against a behaviouristic interpretation of serial learning in monkeys. In a successive set of experiments these authors ([12], experiment 1) introduced 'wild card' items in the serial learning task. Monkeys already expert on the ABCDE sequence were trained with a 'wild card' item (W) that could replace any of the items of the original sequence, thus, forming five additional sequences WBCDE, AWCDE, ABWDE, ABCDWE, ABCDW. In another experiment D'Amato and Colombo ([9], experiment 2) used two 'wild cards' (X and Y), forming 10 different sequences (e.g. AXYDE, XBCYE, etc.). The monkeys reached high accuracy of responses in all the sequences containing 'wild cards'. The rationale for these experiments was that, since the position of 'wild cards' within the sequence was changed, it was unlikely that the monkey's performance was based purely on associations between adjacent items of the list. On the contrary, it seemed more plausible to attribute to the monkeys some knowledge of the ordinal position of the items within the sequence.

The evidence for some form of representation of ordinal position in monkeys has some important implications. In fact, it can be conjectured that if a monkey is able to process information about ordinal position, it might have also the competence to form an abstract template of a serial learning task. The template, once formed can then be used with novel series by filling in, at the appropriate position, each of the items of the sequence in hand. The formation of such a template would result in a positive transfer to successive series containing new items. Such a device would be much more powerful than the ability to form associations between each of the elements of a particular series because the associations developed to learn a unique sequence cannot be exported to new isomorphic problems.

2.3. Successive list learning: relaxing the 'forward' training procedure

Some evidence for transfer abilities on successive serial learning tasks has been presented for rhesus monkeys (Macaca mulatta) by Swartz et al. [51]. These authors trained their subjects on multiple four-item series lists. Each sequence contained different items. While the macaques were learning successive series, Swartz et al. [51] were able to modify the training procedure, eliminating the early phases of training. Thus, while the early series needed to be drilled using the forward procedure described above (i.e. only one item is presented first and then one more item is added to the series and so on), in acquiring successive series, the subjects were able to deal with a training procedure which featured the presentation of more than one element of the list from the outset (for example three items ABC, or the whole four-item series ABCD). Although the performance under this latter training
procedure was mediocre at the beginning, the accuracy steadily increased on each of the subsequent lists. On the basis of their results, the authors claim that some form of hypothesis testing and chunking of adjacent items underpinned the transfer. For example, on lists trained starting with the simultaneous presentation of three items, the performance of the subjects dramatically improved when they became able to identify the first two items (A and B). The authors argue that this result supports the idea that the subjects chunked the first two items and then responded to the item C by default. The same phenomenon was observed in lists trained starting with the simultaneous presentation of four items. In this latter case, the dramatic improvement appeared after the identification of the third item C, so that the fourth item D, could now be responded to by default. These results support the idea that some changes occur in the way in which the representation of the list is organised in the course of task practice. They also indicate that the experience of learning successive lists produces both the formation of abstract templates of ordered items and the ability to assign items from novel lists to particular ordinal positions.

2.4. Forward training and unconnectedness: concluding remarks

Overall, serial learning studies show that, in order to report an arbitrary list of unconnected items, non-human subjects organise the items in memory in more sophisticated ways than a simple associative chaining theory would suggest. However, serial learning studies appear to be chiefly a punctual and opportune reaction to simplistic behaviouristic explanations of the behaviour of complex organisms, and only to a lesser degree an attempt to fully characterise their cognition. As a matter of fact, the original rationale of Terrace and colleagues was not completely dissonant with themes belonging to the behaviouristic tradition. Their aim was to show that apes' linguistic production could have been explained better in terms of associative learning than as the product of grammatical competence. Successive studies focused on the issue of whether response chaining was to be considered the only mechanism responsible for serial learning but the training techniques were still a basic modification of the standard behaviouristic procedure to teach chains of responses. The tension was mainly between the idea that associative response chaining can explain all serial behaviours of all organisms and the questioning of the ubiquity of such a mechanism. The results clearly showed the inadequacy of associative chaining and some alternative mechanisms were proposed. However, not much effort was dedicated to evaluate the possibility that within the class of non-associative mechanisms a variety of different strategies might be explored by different species according to their cognitive status or that a shift of strategy might take place in function of the level of expertise that a subject acquires in the course of task practice. In this latter respect an attempt was made by Terrace and colleagues with their successive list learning paradigm. The formation of a general template for list learning in the course of practice was tested but the process of formation of such a template and its features so far have not been fully characterised.

It can be conjectured that the reason for these restrictions of the research program might lie in the nature of the paradigms used. When the sequence of the items to be learnt is chosen on an arbitrary basis and strict training procedures are employed, the subject has few opportunities to show any ability to impose some forms of organisation upon the items to be reported. A different scenario emerges from studies involving a task featuring items which can be connected on a meaningful basis but where the order of the set is not artificially taught by means of a step-by-step training. It emerges that monkeys, if given enough task practice, do organise the material in ways which allow a better management of cognitive resources both in terms of robustness of the solution and of minimising the memory demands of the task. These studies are based on paradigms traditionally used for the study of transitive inference and will be reviewed in the next section.

3. The five-term series tasks: transitive inference and the emergence of cognitive regulation

3.1. Implicit connectedness and spontaneity

The studies reviewed in the previous section featured tasks where subjects were required to reproduce a sequence of responses to unconnected items in the specific order established arbitrarily by the experimenter. The only information the subject can rely on is the reward contingencies for the specified order of the sequence. On the basis of this invariance (the serial order) the subject can infer, by trial and error, the task requirements.

A different line of research focuses on the problem of how the subjects organise series of items connected by implicit relationships. A paradigm where a series of binary discriminations is connected by the fact that each pair of discriminations shares a common term is based on a task now commonly employed for the study of transitive inference. Here, as we shall see, there exists a relation between the items, but it is not perceivable directly and has to be constructed at a representational level by the subject. As for the serial learning studies the reward contingencies for each discrimination are defined on an arbitrary basis. However, the presence of a common stimulus in every two discrimination problems
makes it possible for the subject to infer an underlying structure of the task which allows the solution of all the discrimination problems without having to store in memory the correct response for each of them. Moreover, this must be done quite spontaneously since there is no explicit feedback which provides an artificial and selective incentive to detect the underlying structure of the task.

A version suitable for comparative studies was used by McGonigle and Chalmers [37,39,6] with squirrel monkeys, to investigate the basis of transitive reasoning within a series of five items connectable on 'symbolic' basis. In order to develop their paradigm, McGonigle and Chalmers modified the conventional five-term series task $A > B > C > D > E$ (originally designed for children by Bryant and Trabasso [5]) so that the same procedure and apparatus could be used with human and non-human subjects.

McGonigle and Chalmers' task involved a training on couples of 'premises' $A + B - , B + C - , C + D - , D + E -$ (where the sign plus indicates reward and the sign minus no reward), presented as coloured containers. The training was followed by a testing phase which featured the presentation of all the possible pairs obtained from the five items ABCDE, in absence of any further differential reinforcement. The authors aimed to assess whether from such a training the monkeys formed an ordered representation of the series $A > B > C > D > E$, which then would have led to transitive choices in the pairs of non-adjacent items of the testing phase. The subjects showed a transitive bias in selecting the appropriate item in the different couples of the testing phases, including the critical pair $B > D$ (the only non-adjacent items equally reinforced and non-reinforced during training).

Findings undermining the assumption that success in this task was necessarily based on logical skills (as previously interpreted, see [2]) came from the liberalisation of the binary restrictions of the task by extending the decision space [37–39]. Once the subjects were proficient with the binary testing, they were presented on a triadic version of the test trials. The triads were obtained by combining the items of the original sequence in order to obtain test trials in the form, for example, of $B > C > D$. The rationale was that if the subjects solved the binary version of the task by means of a co-ordination of each of the pairs of non-adjacent items around a mental representation of the absent middle term, as a logistic explanation of transitivity such as that proposed by Inhelder and Piaget [29] would postulate, then the explicit presentation of this middle item should facilitate transitive inferences. The results clearly showed the inadequacies of a logistic explanation of the monkeys' success. In fact, a dramatic decrement in the transitivity of the choices in the triadic testing was observed.

3.2. Symbolic Distance Effect: the spatial hypothesis

The results reviewed above were choice based assessments of the mechanisms underlying transitive reasoning. Other studies based on decision time analyses have tried to demonstrate that the task is solved by means of the development of a spatial representation of the five-term series. These studies focus on a well-known phenomenon found in reaction times of human subjects when faced with tests of ordering skills: the Symbolic Distance Effect (SDE).

In the context of the five-term series task, this effect has been reported for children by Trabasso et al. [62]. Subjects trained to criterion on items ordered along a linear dimension, such as their size (for example a series ABCDE where $A$ is the smaller and $E$ is the bigger), in the testing phase show a negative correlation between reaction times and the ordinal distance of the items in the series (e.g. the BC comparison takes longer than the BD comparison). In other words, the time required to perform transitive choices is shorter than the time needed to retrieve the premises taught during the training phase. Therefore, the SDE (when observed) runs against explanations which postulate that logical deductions are performed on-line at the time of testing. In fact, if the subjects memorised the premises independently and then retrieved and co-ordinated them during the testing phase, one would expect the reaction times to be shorter for the premises and in general to be correlated with the number of transitive inferences needed by the different comparisons [2].

The results obtained by McGonigle and Chalmers [6,37] did not incorporate an assay of decision times, and therefore they could not address the problem of the emergence of the SDE and of the psychological mechanism that might produce it. When observed by Trabasso et al. [62] the SDE was considered as evidence for the presence of a linear spatial representation of the set of items, which is scanned to find the response to a comparison. The further apart the items are along this spatial continuum, the easier it would be to discriminate them and to find a solution to the comparison. Although this hypothesis implies that no inferences are made at the time of testing, Trabasso et al. [62] argued that subjects

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2The Symbolic Distance Effect has also been evidenced in studies on humans, carried out within the so-called mental psychophysics paradigm. In these studies the subjects are required to compare mentally the dimension of well known objects or animals. For example, in a typical experiment, a subject might be required to answer the question: "What is bigger a cat or a whale?". On the basis of the response time, the underlying representations of the subject and the processes used to compare the different representations are derived. Since the earliest studies [43,45], it has repeatedly been found that the response time of adult humans varies inversely with the distance between the referents of the dimension being judged. So that, for example the comparison of a cat with a cow takes longer than one involving a fly and an elephant.
use transitive inferences during the training phase in order to construct the linear order.

3.3. SDE in monkeys: 'forward' training versus practising connected discrimination problems

In the attempt to identify the basis of possible representation of linear order in monkeys, D'Amato and Colombo [13] tried to elicit the SDE in capuchin monkeys (Cebus apella). These authors assumed that if the SDE was found in monkeys performing a serial learning task, then the effect could have been taken as evidence for the fact that their performance was based on a spatial representational device.

In a first experiment, D'Amato and Colombo [13] trained their subjects to perform an arbitrary sequence of responses using the conventional forward procedure. Then, they tested the monkeys on all the possible pairings of the five terms and registered their response time for pairs characterised by different distances between the two stimuli (such as, AB vs. AC vs. AD vs. AE). The monkeys failed to show a SDE.

The effect, however, appeared in their second experiment, where monkeys were trained on a task based on pairs of connected items as used for the study of transitive inference [37]. In this second experiment the monkeys were trained on couples of adjacent items (AB, BC, CD, DE) and then tested, as usual, on all the possible pairings of the five terms. In order to account for the differences in the results of their two experiments, D'Amato and Colombo were forced to assume that the subjects had at their disposal two different sorts of processes to deal with the serial organisation of behaviour. One is the classical associations chain, which they claim would account for serial learning, and the other is the spatial paralogical device which can explain the appearance of the SDE when subjects are trained on pairs of conditional discrimination (mutuated from an ordered series). They had also to accommodate this latter interpretation to their previous accounts of the results from serial learning experiments and those using 'wild cards' (see previous section).

In conclusion, capuchin monkeys seem to develop more sophisticated forms of representations in situations where they have to find by themselves the relationship between pairs of items belonging to an ordered sequence. By contrast, in a situation where the sequence is rigidly taught step by step, they do not spontaneously devise such a type of organisation.

It is also interesting to note that D'Amato and Colombo obtained the SDE only after the second of two training/testing cycles. The authors interpreted this finding as follows: "It might be possible that the 9 training and 10 testing sessions of their first cycle might non have been sufficient to completely divert these subjects from the associative chain mode of processing, which was the rationale for the second training/test cycle" ([13], p. 137). Thus, overall, it seems not only that items which can be spontaneously organised on the basis of meaningful sequences allow the subjects to construct sophisticated forms of representation of their serial production, but a protracted exposure to the task is required in order to change the form of representation and the processes which act upon them.

A new study on squirrel monkeys by McGonigle and Chalmers [39] provides further information about this issue. The experiments were designed to integrate all the information provided by the presence of the SDE, an assay of the decision times shown in the binary testing, and an evaluation of the performance shown by the subjects in the course of triadic testing. Furthermore, the study featured an extensive presentation of the triadic testing, in order to evaluate possible changes in performance with practice, although in absence of further selective reinforcement.

Evidence for a SDE, was found for both group and individual subjects. And, on the basis of an analysis of the performance and its time correlates in the triadic testing, the meaning of the SDE was reinterpreted. The triadic testing, in fact, allows the testing of hypotheses based on a linear representation of the five-term series. If the SDE is expression of the mental ordering of the set of items A > B > C > D > E, one can expect that subjects who showed the effect in their reaction times should be able to rank the items presented explicitly in a triad such as B > C > D. As for previous studies [37], decrement in performance was observed at the beginning of the triadic testing, as compared with the level of performance achieved on the binary testing. This result suggests that it is unlikely that the performance of the subjects was either based on the co-ordination of non-adjacent items around the middle term or that a perfect linear representation of the set of items was formed during the binary testing.

A further assay of the reaction times showed in the binary testing [39] produced data supporting a novel interpretation of the SDE. If plotted as a function of the end points and not of the distance of the items (i.e. AB, AC and AD vs. DE, CE, and BE), the reaction times formed two populations of scores, one fast (for the pairs including the term A) and one slow (for the pairs including the term E). Thus, the SDE observed in the binary testing can be explained by the fact that, as the distance of the separation between two items increases, the more likely it is that the two items belong to the two different populations of fast and slow responses.

Since task practice revealed to be a factor of primary importance for an accurate evaluation of the competencies of the subjects, McGonigle and Chalmers ([39],
Inadequacy of binary contexts for the study of serial competencies

Overall from the findings of this study it is possible to conclude: first of all that the SDE had been over-interpreted as expression of the presence of scanning processes which operate on an ordered linear representation of a series; and, secondly, that from binary versions of transitivity tests it is much more difficult to infer principled forms serial control. By contrast tasks requiring the organisation of multiple items presented simultaneously seem to be much better proof of the ordering abilities of the subjects.

This conclusion is also supported by the fact that a number of studies, using species as different as pigeons [19], rats [14] and chimpanzees [26], never failed to show evidence of transitive reasoning in binary versions of the task. However, since none of these studies incorporated a time analysis it is impossible to make strong claims about the similarity of the processes underpinning the performance of apes, monkeys and non-primate species. Moreover, to date no one has attempted to demonstrate whether non-primate species, which are able to solve the binary version of the transitive inference task, would be able to self-regulate their behaviour, as monkeys do, in the triadic version of the task.

Even a simple neural network trained and tested on the binary version of the task shows a transitive performance analogous in several aspects to that reported for children and animals [21,22]. Since the output of a system which (apart from its basic architecture) can be considered as a tabula rasa and obviously did not experience either cognitive growth or natural selection, does not differ from that of young children and animals, the comparative relevance of performance shown in the binary implementation of the five-term series task can be seriously questioned. In addition, simple algebraic models, mutated from simulations of bees discrimination learning, have also been claimed to account for the transitive behaviour in this version of the task [9]. By contrast, neither simple connectionist models nor basic algebraic simulations have been elaborated to account for transitive inference in situations involving the presentation of more than two items.

Studies involving both triadic testing and time analyses show that situations where the size of the set is expanded and where items are presented simultaneously represent the best test of the status, the possible function, and the limitations of the ordering abilities of the subjects. The expansion of the decision space has in fact a twofold rationale. On the one hand, it provides a transparent window on the competencies underpinning the performances of the subjects. On the other hand, the problem of facing a large decision space might represent an incentive for the subject to deploy more sophisticated strategies in order to cope with the increased demands of the task.

However, to implement research projects which meet these requirements a paradigm shift is required. Tasks based on binary choices fail to provide the dynamic spectrum of different strategic solutions and their possible changes over time as a function of gaining task expertise. Serial learning tasks seem inadequate too. The rigid training imposed on the subject does not leave enough freedom to evaluate the spontaneous interplay of different regulatory functions. The arbitrariness of the sequences, moreover, does not offer enough constraints for the subjects to impose some form of organisation on their serial production.

Tasks are necessary which allow the subjects to spontaneously express strategic factors and a better management of the amount of data to be retained to solve the task. These should feature situations which go beyond the binary context and, in contrast with tasks requiring the acquisition of arbitrary lists, where the elements for
Solving the task are available to the subject from the outset and do not have to be found inductively by trial and error.

Along these lines, some new paradigms based on search tasks are currently being developed. The first attempts of implementation and some preliminary results will be outlined in the next section and compared with more traditional research approaches focusing on search.

4. Search tasks: the spatial organisation of serial productions

4.1. Why search?

Tasks requiring the exhaustive search of a set of loci can be considered a way of studying serially motivated behaviours in situations which avoid the shortcomings detected in the paradigms reviewed so far. The rationale rests on the fact that search has implicit serial components (the subjects have to perform each move one after the other), and each locus to be explored can be connected in a meaningful way to the others by its relative spatial position and distance or by other relations. In this situation, the analysis of the succession of moves should reveal the organisation of the serial production of the subject.

Search tasks also have an implicit memory component. To search efficiently, and avoid searching again in locations already explored, the subject has to keep track of the moves already performed. In this respect, precise measures (both quantitative and qualitative) of the behaviour of the subjects are warranted. First of all, since success is defined unambiguously as the ability to perform exhaustive searches, an objective criterion for its achievement is granted (i.e. the subject exhausts the set and obtains the peanut); then within the success space, there is a range of more or less efficient searches again suitable to be measured objectively. In fact, whereas an optimal search would produce only one visit per each location, non-optimal searches result in some reiterations on locations already visited. Thus, the ratio between the number of loci faced by the subjects and the number of moves performed to exhaust the set (i.e. the percentage of non-redundant moves) provides an index of the relative efficiency of behaviour within the success space. Each surplus move has a cost attached and the task implicitly provides the currency in terms of time (and/or energy) spent in searching before obtaining rewards. As a consequence the subject has a source of feedback information to evaluate the relative economy of successive searches. The change in the percentage of non-redundant moves over time reveals how much the subject is regulating its behaviour in absence of any selective feedback provided artificially by the experimenter.

The qualitative analysis of the search trajectories, provides information on the serial organisation, if any, of the search behaviour of the subjects. A relationship can be hypothesised between the serial component of the task and the memory load: a configuration of loci which presents particular structural properties allows principled searches to be used as a sort of notational system. An example is a linear arrangement of loci. In this situation a subject who starts a principled search from one end to the other, moving always to adjacent loci does not have necessarily to memorise the moves already performed. The particular point of the trajectory the subject is in, at a given moment will tell unambiguously the loci already explored and those which remain to be explored. On the basis of these observations it can be conjectured that serial order (a particular trajectory through the search space, e.g. start from location A, then move to B etc.) can emerge spontaneously as an attempt to reduce the memory demands of the task. Such serially organised behaviour contrasts with an unprincipled search featuring successive moves performed in a random order. In this latter situation a subject to avoid redundant moves needs to memorise each of the locations it explores while searching and would inevitably fail to avoid redundant moves when the number of loci to explore surmounts the memory span.

4.2. The problem of involuntary cues in primatological search studies

In a classical study, Menzel [42] showed that chimpanzees are able to remember most of the hiding places (12.5 out of 18, in average) of items of food within a large outdoor enclosure and that they use trajectories which reduce the distance of travel below chance level. Moreover, analysing the search behaviour of the apes in each trial, Menzel found that the frequency of repeated visits to locations already explored was practically negligible.

However, it is likely that the animals in this experiment when retrieving food left involuntary but recognisable cues of their visits. In an experiment designed to restrict the “use of cues other than distant vision [...] almost completely”, each piece of food was dropped in the grass and was not “covered up further” ([42], p. 945). With this procedure only four items of food where hidden in four different locations and even with such a small search space the animals failed to perform exhaustive searches in almost half of the trials (11/24=46%). The number of repetitions to locations already visited is not reported for these trials.

More recently the relationship between memory and search behaviour of yellow-nosed monkeys [33] and gorillas [32] has been investigated. In both studies the animals were presented with a set of eight cups. According to the different conditions of the experiment
either all the cups or a sub-set of four of them were baited. In the first condition, where all the cups were baited, the authors consider as evidence for a good memory the fact that the subjects performed exhaustive searches of the set of containers without revisiting previous depleted food sites. MacDonald [32] admits explicitly that the fact that the displacement of the containers after each of the visits might have provided cues to avoid repetitions. The same flaw is present in the first study by MacDonald and Wilkie [33]. Therefore, the data referring to the ability of non-human primates to perform exhaustive searches within a set of containers are flawed by the particular apparatus used which provides unequivocal cues to the animals for locations already visited. Yet a measure of reiteration is essential if we are properly to evaluate the extent to which subjects can keep track of choices made serially over time.

4.3. Search strategies in the standard radial maze

Following the pioneering work by Olton and Samuelson [44], an enormous amount of research has been conducted on search abilities of animals (chiefly rats) running the radial maze. The radial maze, consists in a central platform, from which a number of arms (originally eight) depart in a radial fashion. In the basic procedure (of which, as we shall see, many variants have been developed) each arm is baited and the rat can freely explore the maze to collect them. Therefore, the most efficient behaviour for the animal would be to perform an exhaustive search of the arms avoiding revisits to those already visited. In this apparatus it is possible for the subject to deploy an algorithmic strategy consisting (as for the example on the linear array outlined above) in visiting in succession adjacent arms following a particular direction of travel (e.g. clockwise). However, since the traditional interest of researchers using radial maze based procedures was the assessment of the memory span of the subjects, the degree of retention after delay, and the type of coding involved, the researchers have usually tried to devise tasks which cannot be solved by data-reducing strategies. A classical example of a procedure which controls the possibility that animals rely on algorithmic strategies in order to solve a radial maze based task is the forced choice. The animal is forced (by blocking some of the arms of a maze) to explore only a sub-set of the arms in a first trial. It is then allowed to search again. Since food has not been replenished the rat should now search in the sub-set of arms which were not visited on the first trial. Since in this second trial the arms containing the bait are not always adjacent ones the subject is discouraged from using strategies and it is forced to rely on brute memory for the locations explored in the first trial or those which remain to be explored.3

However, an evaluation of results obtained with children tested with the radial maze shows that even the deployment of a simple algorithmic strategy is not a trivial matter and that its use parallels cognitive development. In fact, not only differences in performance emerge in an eight-arm radial maze between 2 and 4 year old children, the 2 year olds performing marginally above chance and contrasting with 4 year olds who rarely revisit previously explored arms [23], but also relevant differences between the two age groups emerge at a qualitative level of analysis. While older children spontaneously deploy algorithmic strategies such as making successive responses to adjacent arms, younger children do not use any strategy from the outset. Although evidence for a developmental trend in the use of strategies emerges from their data, the authors main interest in the problem of spatial encoding leads them to discourage the use of this strategy by “turning the subject at a random angle with the eye closed upon return to the centre between choices” or by using a version of the forced choice procedure. Interestingly, the number of redundant choices performed in the forced choice condition (now that the subjects have to search only four locations on trial 2) increased for the older children and decreased for the younger. It can be concluded from this data that older children relied more on strategies than on brute memory for the location explored and the opposite applies to the younger subjects whose performance improved when the use of an algorithmic strategy was hindered.

The relationship subsisting between the emergence of serially based search strategies and age in humans is supported by the results of another study conducted with 1, 5, 5–6 year old children and adults, running a version of an eighth-arm radial maze [1]. In contrast with previous studies [23], this work was specifically motivated by the hypothesis that human performance in the radial maze is more dependent on search strategies than it is for rats and that the ability to search strategically follows a developmental trend. It was observed that accuracy of performance in a free choice condition increased with age in parallel with the measures of

3A different procedure involves removing the animal from the maze after it has visited a certain number of arms. After a delay, the animal is reintroduced in the maze and its ability to avoid revisits to the arms it had already explored is evaluated. By means of this procedure and by means of an analysis of the relative effects of delay interposed at different points of the search sequence, it has been shown that rats use either retrospective (i.e. they remember the arms already visited) or prospective information (i.e. they remember the arms which remain to be visited). Although, a shift from retrospective to prospective coding as a function of the Point of Delay Interpolation [8] can be considered as a form of data reducing strategy, an evaluation of this literature is beyond the scope of the present study which is confined to the relationship between serial order and memory.
sequential organisation of search, such as entering four arms in sequence in the first four choices. Forced choices conditions which prevented the use of search strategies reduced accuracy only in older children and adults. Among the strategies selected by the children the authors also found a developmental trend in the tendency to start search from a fixed location. A similar trend was observed in the use of a strategy based on always moving to adjacent arms. Moreover, in the subjects who used these two strategies, the tendency to use consistently the same direction of travel was observed.

4.4. Serial order and mnemonics

Experiments based on search tasks and explicitly aiming at the study of the emergence of serial order in search have recently been implemented using touch-sensitive computer monitors and a large indoor enclosure. Touch-screen based tasks [40,15,16,63] are search tasks where subjects are required to respond to each icon of a set presented simultaneously on the monitor. So long as the search is exhaustive, the task requirements are achieved and a peanut is dispensed as reward. In other words the only task requirement is to touch all the icons on the screen.

In one of the spatial versions of the task the subjects are presented with a set of 9 identical icons spatially arranged according to a 3 x 3 matrix. The subjects are not trained to follow any arbitrarily defined trajectory through the set but are left completely free to select the items in any order and are allowed to reiterate on items already touched. Thus, the task warrants a variety of solutions (i.e. the different trajectories of travel through the search space) from which the subject can spontaneously choose and a richer set of principled searches (i.e. each involving a fixed starting position, an adjacency and a vectorial principle) is possible in such a search space compared to the radial maze.

Six capuchin monkeys (Cebus apella) tested in this condition proved to be able to perform exhaustive searches in a number of moves much inferior to that expected by chance [15,16,40,63]. Moreover, given the opportunity to practice the task, they showed a significant trend in the reduction of the total number of moves performed to complete each search. An analysis of the trajectories followed by the monkeys through the search space revealed some organisational principles underpinning search performance. The monkeys started their searches from a sub-set of all the possible locations, moved on adjacent items more than expected, and, at a more qualitative level of analysis, showed the tendency of moving along preferred vectors of travel (e.g. the frequency of transitions left to right and bottom up is significantly larger than transitions performed in the opposite directions).

The behaviour of the monkeys contrasts with both the behaviour of children and that shown by pigeons tested in the same task. Four year old children perform very economic and principled searches when presented with the 3 x 3 matrix ([40,57]; these results are also described in [63]). Their economy of search is maximal (approximating the 100% of non-redundant moves) and their trajectories of search are characterised by a perfect axial organisation (e.g. they complete the search of each column of the matrix before moving to the next column). By contrast, in a similar task pigeons seem to move at random among the icons and are not able to perform exhaustive searches in configurations featuring more than five icons. Monkeys seem to fall somehow between these two extremes. They perform relatively economic searches and their trajectories of searches conform to some principles (fixed starting locations, adjacency etc.) but they are never as principled as those shown by children, although their behaviour is less chaotic than that observed in pigeons [15,63].

It seems, therefore, that the ability to impose a structure over a 3 x 3 matrix is a dimension of relatively great comparative relevance compared with series length in a serial learning task or the presence/absence of the ability to show transitive 'reasoning' in the five-term series task. However, in this task, since the subjects were allowed to make redundant moves, the high variability of the search length for each trial prevented the detection of constant characteristics of the serial production of the monkeys which would have allowed a better characterisation of their behaviour.

Additional data concerning the role of organisation in search comes from a time analysis of the behaviour of the monkeys in another condition of the touch-screen based experiment outlined above. Originally, this kind of analysis was motivated by a consistent phenomenon observed in adult humans when required to report lists of items (ranging from single letters or numbers to words of different lengths) previously presented on a computer monitor [49]. In this situation a positive correlation is typically observed between the length of the list to be reported and the averaged inter-item interval during retrieval. The finding has been interpreted as evidence for the presence of motor planning, as opposed to simple chaining of responses as a behavioural account of the process underlying serial retrieval would postulate. In fact, a chaining hypothesis would suggest that the production of each component of the list to be reported is elicited by the stimulus provided by the response to the previous one. This latter process is local and always the same for different list lengths. Therefore, it cannot explain a difference in latencies as a function of global features of the list to be reported. On the contrary, more sophisticated processes used to organise the items in memory, to detect, retrieve and report them, might well be sensitive to global features of the list such as its length or its structural properties.
The hypothesis that the same argument could have been applied to the search behaviour of the monkeys was tested by presenting the animals with a condition where blocks of trials featuring a different number of icons were interspersed within each experimental session. In this experiment the task requirements were the same as those of the experiment described above: the subjects had to touch each of the icons (identical to each other in everything but the spatial position) presented on a touch-screen. As long as the search was exhaustive, a peanut was dispensed as reward. The only variable which made the experimental conditions different to each other was the number of icons featured by the set (and, obviously, the fact that there were more empty locations on the screen when less icons were presented). In this experiment, a positive correlation was observed between the averaged inter-touch interval (delay between the touching of two icons in succession) and the number of stimuli presented (ranging from 4 to 9 items and displayed in random positions within a virtual $3 \times 3$ matrix). This phenomenon supports the motor planning hypothesis rather than the chaining hypothesis. Furthermore, the results allow the conjecture that the increase in the number of icons to be explored provides more incentive towards the organisation of the motor behaviour. If it is true that monkeys somehow deploy more organisational principles when faced with larger search spaces, this result could be taken as evidence for some precursors of human metacognitive skills in non-human primates. Monkeys would be able to detect the intrinsic difficulty of a large search space and devote more effort towards searching it strategically in order, for example, to reduce the memory load imposed by the task.

However, in this situation the increase in the number of icons parallels an increase in the spatial structuration of the configurations. In fact, whereas a configuration with 9 icons fills up the $3 \times 3$ matrix, a configuration containing less than 9 icons leaves some of the loci unfilled. Consequently, the question remains ambiguous as to whether a higher degree of organisation is motivated by the form of the configuration or by the increase of the number of icons to be explored.

4.5. The manipulation of the spatial configuration of the search space

The role played by the form of the configuration to be explored on the economy of search of capuchin monkeys was addressed in another experiment [17,18] based on search tasks implemented in a larger-scale environment. The experimental set-up features a number of containers hanging from the ceiling of a large indoor cage ($9 \text{ m}^2$). In each of the containers there is a fragment of peanut and the monkey has to recover each item of food by searching serially among the containers. In this situation it is possible to assay the number of exhaustive searches spontaneously performed by the subjects and, as in the touch-screen based search tasks, the number of redundant moves performed before completing the search. The spatial arrangement of the containers can then be manipulated in order to evaluate which form of configuration sustains more economic searches.

In the first phase of the experiment, four capuchin monkeys where tested for 60 trials on a configuration similar to the one presented with the touch-screens: a matrix $3 \times 3$ of small plastic containers. The aim of the first phase was twofold. On the one hand the comparison of data obtained in a foraging-like situation with those obtained using computer monitors seemed particularly interesting to evaluate the generality of these latter results in situations with a more explicit ecological value. On the other hand, this phase would have provided a baseline condition for the following phase in which the spatial configuration of the cups would have been manipulated.

The monkeys spontaneously performed exhaustive searches in the vast majority of trials (60/60, 58/60, 55/60, and 53/60, respectively, for each of the individuals). The percentage of non-redundant touches was in average 53.8%, slightly larger than that observed in the first 60 trials of the touch-screen based experiment (49.1%) and remained constant across sessions of training. The improvement in the economy of search as compared with the touch-screen based experiment can be explained on the basis of the fact that using the suspended containers apparatus negative feedback (the absence of reward) is provided implicitly to the monkeys by each reiteration on locations already explored. By contrast, in the touch-screen based experiment, the feedback was provided exclusively at the end of the trial, and the subject lacked immediate negative feedback on the redundant move just performed. Moreover, one can conjecture that the increased distance between the loci to be explored adds costs to each reiteration and this acts as an incentive towards searching in economic ways.4

In the second phase of the experiment the relative

4It can be claimed that the touch of the icons on the screen with no actual locomotion is a substantially different spatial task as compared to visiting places. When faced with a computer monitor, the subjects could rely more on an allocentric spatial code, whereas egocentrically defined positions could prevail when the subject enters physically into the search space. Nevertheless, the main issue addressed by both experiments is the relationship between the organisation of search and memory, regardless of an accurate description of codes used by the subjects to represent spatial locations. A similar argument would apply to the issue of prospective and retrospective coding [8]. The question of the type of processing used by the monkeys in the search tasks described here would be of extreme interest. However, it was not addressed in these experiments and it is neutral to the issue of the overall relationship between organisation of search, memory load and performance.
distance between the cups was manipulated so that the search space was divided in three clusters of three cups each (the distance within a cluster being of 35 cm, and the minimal distance between clusters being of 110 cm). The rationale of this phase was to evaluate the relationship between the presentation of a search space which can be organised in chunks and the memory for the locations already explored. In fact, if principled searches are performed in this situation (exhausting a cluster before moving to the next) the subject needs to keep in short-term memory only three items at a time (the three loci within a cluster and then the three clusters). By contrast, a random search between the loci, without chunking them, has to be sustained by brute memory for each of the loci (nine items).

In this condition a dramatic improvement in the economy of search was observed (77.1% non-redundant moves in the 60 trials presented) when compared with that obtained in phase one (53.8%). A strong linear trend in the reduction of redundant moves was also observed, the averaged percentage of non-redundant moves performed by the monkeys during the last ten trials of testing reaching 90.6% (0.93 redundant move per search). Moreover, a qualitative analysis of the search trajectories spontaneously selected by the monkeys shows strong preferences towards completing the search of the three icons within a cluster before moving to a different cluster.

Therefore, there is strong evidence for the fact that monkey subjects are able to exploit the spatial constraints of a configuration which can be organised in spatial chunks or 'patches'. In fact, in absence of any explicit instruction their search differs from a random walk among the loci to be explored and follows a very organised serial production. This consisted in moving (above chance) within each cluster before shifting to a new cluster.

A third condition was also implemented to control for the possibility that the improvement in the economy of search shown by the monkeys in phase 2 was merely due to task practice. Another 60 trials were presented featuring the same configuration used in phase 1 (3 x 3 matrix). Here the performance of the monkeys collapsed at levels analogous to those observed in phase 1 (59%), thus confirming that the improvement observed in phase 2 was due to the form of the configuration.

Although a number of experiments have addressed the issue of how hierarchical organisation can affect search behaviour of a variety of species [46], no systematic attempts have been made to compare different species with a paradigm involving the alternation of conditions featuring different spatial configurations of the search space. However, an evaluation of results obtained from different studies (and therefore only partially comparable) suggests that different species show a different level of economy of search as a function of the spatial constraints of the search space.

The role played in the organisation of search behaviour of rats by spatial chunking under various spatial arrangements of maze arms has been studied by Shenk et al. [48]. Along with other things, it emerged from this study that rats worsen their performance (measured in terms of redundant moves to arms already visited) in 9- and 8-arm mazes which afford 3 and 2 chunks, respectively, by virtue of angular relationship between the arms, as compared with standard radial mazes of comparable number of arms. These results strongly contrast with those obtained with monkeys in the experiments outlined in the previous section which by contrast improve their performance in situations affording spatial chunking. However, differences between the two experiments must also be stressed. For the maze each of the chunks featured different angles between adjacent arms, whereas the distance separating the clusters in the experiment with the monkeys remained constant for different triplets. This difference between the overall structure of the search space in the two studies might be of particular importance since Shenk et al. found that rats made selective errors in function of the shape of the chunk (e.g. parallel arms leading to the majority of errors). Moreover, a standard radial maze might afford easier algorithmic solutions than a matrix or a set of cluster of loci. In fact in a radial maze the reiteration of a single response (e.g. when exiting an arm move left) would produce errorless exhaustive searches.

As a further comparative note it is interesting to consider that pigeons confronted with the task of performing a search within different configurations of keys on a panel perform better when they are arranged as a matrix than when they are presented as a linear array [65]. Since apparatus and procedures adopted in this study were quite different from those used in the radial maze based studies in rats, the results are not perfectly comparable with those obtained by Shenk et al. However, it is interesting to highlight an analogy between the difficulty encountered by rats in exploring parallel arms in a maze and the difficulty found by pigeons with a linear array set. From the perspective adopted here a linear array would afford strategic searches from one end-point to the other. Such a principled search would require a minimal amount of memory. The assessment of the ability of monkeys to organise searches on a linear arrangement of loci would be of extreme interest, in order to evaluate the hypothesis that primates regulate their behaviour under a variety of

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1A number of studies (e.g. [27,7,24,10]) are evidence indeed of a positive relationship between chunking and memory in the rat's search behaviour. Nevertheless, a proper evaluation of this literature could not prescind from an analysis of the variety of apparatuses, procedures and measures adopted which for reasons of length cannot be included in the present work.
stimuli conditions which afford a strategic organisation of search. It is shared here with Shenk and colleagues the conviction that the best way of addressing this question in a comparative framework is the assessment of the spontaneous organisation of search behaviour in various configurational structures. However, whereas they propose that animals' rule-directed movements are finely tuned to particular situations to which they have adapted [48], the hypothesis which is proposed here is that this might apply better to some species than others. The flexibility to elaborate search strategies for the exploration of different configurations of loci might be a function of the cognitive status of the species.

To date no experiments have been conducted to compare the search behaviour of different species with an apparatus such as that featuring a suspended set of containers which allows the flexible manipulation of the spatial configuration of the search space in the absence of cues left involuntary by the animals for each choice. However, any inaugural attempt would be of extreme interest. In fact, the results obtained in the 'patchy' search space show that monkeys are able to exploit the spatial constraints of such a configuration and this sustains a very high economy of search. However, as we have seen capuchin monkeys are not fully competent to do so when the search space features a matrix of loci. Confronting other species with such a configuration one might find an answer to questions such as the following. Does a 'patchy' search space have in itself structural properties which make it easier to explore by a variety of organisms? Is it easier to explore only for particular species because they have been shaped by evolution in accordance with some specific requirements of their ecological niche? Why do monkeys find it difficult to organise their searches within a 3 x 3 matrix while four-year-old children do not? Why do pigeons find it difficult to explore economically sets featuring more than five items? Is it because species characterised by a higher level of cognitive complexity are able to impose a structure over a search space which remains unstructured for simpler organisms? Is the organisation of search just a particular instance of a general problem of information management posed by a variety of circumstances in which long sequences of actions have to be performed? Do metacognitive skills play any role in it as an expression of the attempt to avoid the overloading of the memory system?

5. Conclusions

Overall, a critical look at the literature seems to indicate that from the study of serial aspects of behaviour new dimensions, relevant to the comparative study of cognition, can emerge. Several results point towards the conclusion that serial behaviours are supported by complex competencies and not merely by associative chaining. Therefore the study of the way in which such behaviours are organised might be particularly fruitful in determining different control strategies which different organisms have developed to solve the problems posed by the production of long series of responses. However, in order to make these mechanisms more transparent, some requirements should be satisfied in the choice of the experimental paradigm. In particular, the use of paradigms featuring multiple items, which can be connected on the basis of meaningful relationships, and where a high degree of spontaneity is granted to the subject, seems to represent the best policy for programs aimed at the characterisation of the cognitive potential of primates, as well as that of other taxonomic groupings in the realm of serial behaviour. In fact, it seems that when serial learning is considered on the basis of sequences of unconnected items and where the order of the components is arbitrarily defined by the experimenter, the subject is left with few strategic possibilities to organise its behaviour in ways which are fitted to the task. These take the form of chunking the lists to be recapitulated on the basis of the temporal contiguity of successive items. When monkey subjects have been tested on successive list learning, evidence also emerged for some forms of transfer, based on the formation of 'empty' templates, which can be then filled up by the particular list at hand. However, further research is certainly needed for a better characterisation of these templates, which to date remains relatively unspecified.

Within the serial learning framework, the few studies which have used structured material to be organised in sequences have produced results which allow some richer interpretations of the processes which underlie the performance of the subjects. For example forms of 'chunking' not based merely on temporal contiguity were observed in pigeons, when the possibility of classifying was offered to the subjects. This form of chunking based on classification produced a better performance as compared with chunking based merely on temporal contiguity. Therefore, it can be assumed that paradigms featuring unconnected items force the subject to rely on more demanding and less effective processes and obscure important cognitive potentialities of the organism under examination. This assumption finds further support in results obtained from recent researches [15,41] which used a hybrid paradigm which shares some features with classical serial learning ones but, at the same time, gives the subject the possibility of organising the list to be reported on the basis of classificatory schemes. In this paradigm, monkeys (Cebus apella) are taught to touch a series of icons (differing multidimensionally from each other and presented on a touch-screen) in a fixed order, such as ABC. Then in a transfer phase they are confronted with a configuration featuring multiple exemplars of each category such as AAABBBCC. Here the
subject must touch exhaustively the icons of the set, being free to select the order of interrogation of icons within a category but penalised (omission of reward) if they do not observe the prescribed order ABC between categories. Using this procedure it was possible to demonstrate the ability of capuchin monkeys to perform series of (so far) twelve items. This is a serial production much longer than those recorded for capuchin monkeys trained on unconnected items, which do not exceed five items (e.g. [11]).

The studies on transitivity, using series of connected binary discriminations, show that when a set of five items has an intrinsic ordered structure, the subjects are able to detect it and organise the items accordingly as expressed by their transitive behaviour. However, the mechanisms on which this ordering is based become more transparent when the paradigm shifts from the binary to the triadic context. Here, strong evidence was provided for the fact that logical competencies are not required for transitive reasoning. By contrast, it seems that some forms of rational decision-making, based on the ranking of rules of selection to a sub-set of the items of the ordered series, allow a satisfactory solution to the task. Furthermore, such organisation of behaviour seems to emerge quite spontaneously, when the subject is given enough task practice, as a strategy aimed to reduce the amount of memory resources required to solve the task.

Altogether, these results strongly suggested the need for the use of experimental situations where the subject, in the course of protracted testing, is left free to serially organise a large number of items presented simultaneously, and which hold meaningful relationships between one other.

Recent studies, designed according to this rationale show that search tasks satisfy these requirements. Search is by definition a serial enterprise, the items are connected to each other by spatial relationship, and the subject is left free to exploit these spatial constraints. Moreover, given the simplicity of their implementation, search tasks allow a protracted presentation of the task. The emphasis on task repetition seems to be particularly relevant for the understanding of the extent to which different organisms are able to regulate their behaviour. Only by allowing the subject to become expert with the task, does one give it the chance to recognise the relevant aspects of the situation at hand and the opportunity to self-monitor its own behaviour in order to recognise the possible limitations of its cognitive resources (for a discussion of a similar point of view see [3]).

By means of touch-screen based search tasks it was possible to demonstrate for the first time in a laboratory study that monkeys learn to reduce the number of redundant moves in their serial production, in absence of any explicit feedback provided artificially by the experimenter. They seem to be able to regulate their serial production by monitoring the delay or the amount of energy (for a discussion of the relative role of time/muscular effort in foraging strategies see [25]) inevitably associated with the production of redundant moves. There is also evidence for the fact that their relative economy of search is supported by organisational factors which go beyond simple associative chaining, and that the length of the serial production represents per se an incentive towards organisation. However, even after protracted exposure to the task monkeys are never as principled as children in searching a $3 \times 3$ matrix of loci. Therefore, it seems that important cognitive differences emerge when a spatial structure has to be imposed over a relatively unstructured search space.

The manipulation of the spatial configuration of the set to be explored, nevertheless, shows that monkeys become much more principled and economic when confronted with a 'patchy' search space offered in larger-scale environments. Here they show a very high efficiency of search and a very principled, albeit not stereotyped behaviour. Further comparative data collected in similar situations are needed. In fact, by means of search paradigms in which the spatial configuration of the search space is skilfully manipulated, it should be possible to evaluate the extent to which different species are able to flexibly impose their forms of organisation over a relatively wide range of structurable material. At the same time it might be possible to identify species which have been shaped by evolution to deal with very specific forms of stimulus structure.

Assuming that serial behaviours pose problems of information management in the vast majority of animal species, it might be possible ultimately to pose the question of whether lower organisms have solved the problem of serial organisation of behaviour by coding genetically fixed patterns of actions which support long sequences of actions without any need for memory and decision-making, whereas other species have invested in cognitive complexity to be able to evaluate the limits of their cognitive competencies and compensate them with strategic interventions.

According to McGonigle [35] one of the most important cognitive dimensions (and thus along which different species can be compared) is the extent to which a particular organism is able to individuate, on the one hand, the limitations of its cognitive resources, and, on the other, the relevance of their strategic use in different tasks. In other words, the ability to deploy strategic skills and to self-regulate, a competence that has recently received much attention as an index of cognitive growth in the context of human cognitive development [20,3,39]. In short, the comparative study of the serial organisation of multiple connected items might open the way to a better understanding of the evolutionary path towards the emergence of human metacognitive skills.
Acknowledgement

I would like to thank Brendan McGonigle whose guidance helped form the rationale of this work. Nevertheless, the responsibility for any weakness in the ideas here expressed is, of course, only mine. This work was supported by a fellowship from the Italian Ministry of University and Technological and Scientific Research, and by a FSE/CNR fellowship.

References

[45] Paivio, A., Perceptual comparisons through the mind's eye, Memory Cognition, 3, 6 (1975) 635–647.