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Temporal characteristics of iconic memory

THE duration of visual persistence (iconic memory) is inversely related, up to a point, to the duration of the inducing stimulus. This suggests that iconic memory can more properly be identified with ongoing neural processes than with the decaying contents of a sensory store. Since the publication of Sperling's influential monograph¹ there has been general agreement that a relatively faithful representation of a visual display remains perceptually available for several hundred milliseconds after the distal stimulus has vanished. This led to the postulation of a short-term visual store, also called iconic memory² or sensory register³, with contents decaying rapidly after the termination of the inducing display. The terms visual persistence or icon are commonly used to refer to the perceptual availability of the decaying contents of the sensory store. Iconic memory is regarded as having temporal combinatorial properties which allow perceptual integration of two or more sequential displays even if separated by a brief temporal gap. Integration in iconic memory was convincingly demonstrated in a study where the subjects were required to identify which element in a briefly-displayed array of 16 alphabet characters had been singled out by a temporally trailing bar marker⁴. Temporal integration has also provided an explanation for some aspects of visual masking⁵ and for temporal integration of patterns whose parts were presented sequentially in time^{6,7}. Here I question the view that iconic memory is a store whose contents begin to decay when the inducing stimulus is terminated. I suggest that the duration of iconic persistence is linked to the duration of visual processes which begin at the onset of stimulation and continue for a given duration, whether or not the inducing stimulus is still on display. This view is based on the finding that the duration of visual persistence is negatively related to the duration of the inducing stimulus.

The experimental technique⁷ used a computer-driven oscilloscopic display (gridless Tektronix 602 equipped with ultrafast P15 phosphor) consisting of a square matrix of 25 dots arranged in five rows and columns. One of the 25 dots, chosen randomly on every trial, was not plotted. The subject, who sat in a dark room, initiated each display with a button press and then reported the matrix coordinates of the missing dot. The matrix was displayed in two successive portions separated by a temporal gap: first, an aggregate of

12 dots, chosen randomly from the matrix, was displayed for a period that varied between 10 and 200 ms, depending on the condition; next, a 10-ms temporal gap was allowed to elapse with no dots shown on the screen; and, finally the remaining 12 dots were displayed for 10 ms.

Figure 1 shows the results for two subjects. Almost identical results were obtained with other subjects and with casual observers in the laboratory. A marked impairment in performance is evident as the duration of the leading display exceeded about 100 ms. The phenomenal appearance of the display should be noted: at the shorter durations of the leading portion all dots in the matrix were perceived simultaneously with no evidence of a temporal gap. At the longer durations the display was seen clearly in two successive portions separated by a significant gap.

Since the experimental task was practically impossible unless the two portions of the display were actually seen as one, it seems likely that some sort of visual persistence was necessary for bridging the temporal gap. But could persistence be attributed to the rapidly decaying contents of an iconic store? Probably not. Bearing in mind that the temporal gap was of the same duration in every condition, and that a 'storage' theory assumes an icon whose strength does not start decaying until the termination of stimulation, it is difficult to see how the briefest (10 ms) display could induce iconic contents capable of bridging a given temporal gap while a much longer display could not.

More plausible inferences about visual persistence are, first, that its duration may be more closely timelocked to the onset than to the termination of the inducing stimulus, and second, that it may be more properly considered to be

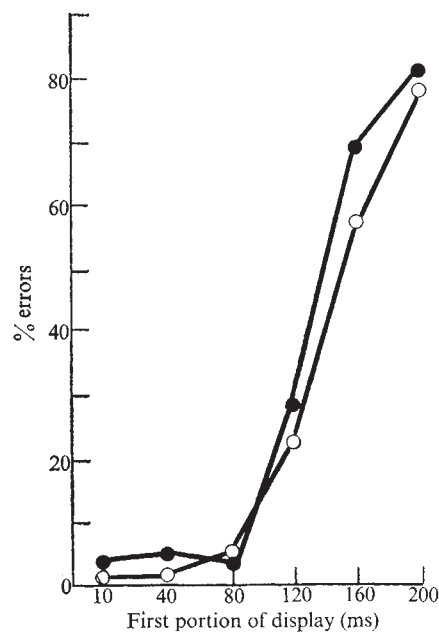


Fig. 1 Percentage of errors in identifying the location of a missing dot within a 5×5 -element dot matrix which was displayed on an oscilloscope in two portions of 12 dots each, separated by a 10-ms gap. The duration of the first portion of the display is shown on the abscissa; the second portion was always 10 ms. The matrix subtended approximately 6° of visual angle. The two portions of the display were equated for brightness through computer-controlled modulation of the oscilloscope's Z-axis. This allowed independent variation of the intensity of each dot in the display. The appropriate intensity levels for each duration of the leading display had been determined separately in a preliminary psychophysical task. Entirely similar results were obtained without brightness-compensation despite some degree of brightness-mismatch between the two portions of the display. Results are for two subjects—M.K. (●) and V.D.L. (○).

a product of ongoing neural processes of finite duration than the contents of a sensory store.

But before pursuing this line of reasoning, an alternative interpretation must be examined. It may be argued that impairment of performance at the longer durations of the leading display (Fig. 1) may have been due not to reduced visual persistence but to the triggering of some form of discontinuity-detection mechanism within the visual system which effectively segregated the two portions of the display one from the other^{6,8}. To examine this alternative, the display sequence was altered so that each of the 24 dots was displayed once only in random sequence at a regular inter-dot interval (with one exception as noted below). If the inter-dot interval is such that the total duration of plotting of the 24 dots exceeds about 120 ms, the matrix appears to have more than one missing element⁷. The observer is thus confronted with a choice among several apparently empty matrix locations which are indistinguishable from the truly empty location. Over 90% of the errors result from confusing the unplotted dot with dots plotted more than about 120 ms before the termination of the display and hence perceptually unavailable⁷.

The procedure of the second study was a modification of that of Hogben and Di Lollo⁷. The inter-dot interval was fixed at 10 ms corresponding to a total (24-dot) plotting duration of approximately 230 ms. In the control condition each of the 24 dots was plotted once only for 1.5 μ s. In the experimental condition each dot was plotted for 1.5 μ s except for the 12th dot which was plotted for 100 ms (Fig. 2). On the assumption that, up to a limit, the duration of visual persistence is inversely related to the duration of the inducing stimulus, it was expected that the sensory persistence of the 12th dot would be briefer in the experimental than in the control conditions. In turn, it was expected that the 12th dot would be erroneously identified as missing more frequently in the experimental than in the control conditions.

Two observers (the author and a student unaware of the purpose of the research) served in five experimental and five control sessions; each session consisted of 100 trials. The error distributions are shown in Fig. 3, separately for each

Fig. 2 Schematic representation of the plotting sequence. Each of the 24 dots was displayed for 1.5 μ s except for the 12th dot which was plotted for 100 ms. The 12th dot remained on view from the time of plotting of the second dot until 10 ms after the plotting of the 11th dot. Its brightness was indistinguishable from that of all other dots through the compensation procedure described in Fig. 1. The order of plotting was randomised on every trial so that every matrix location had an equal probability of being the 12th in the sequence.

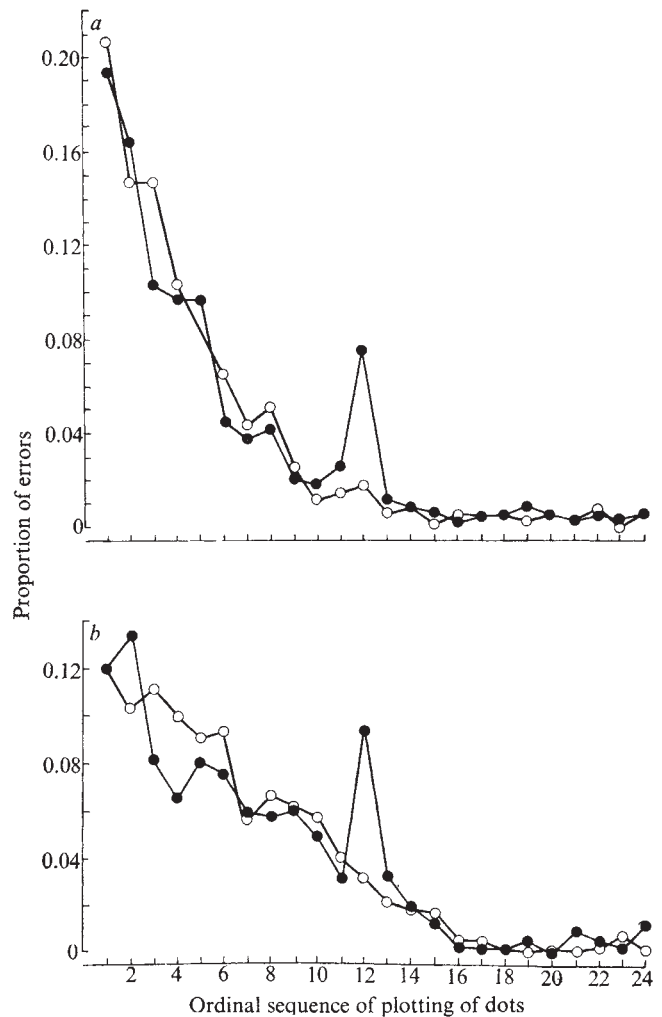
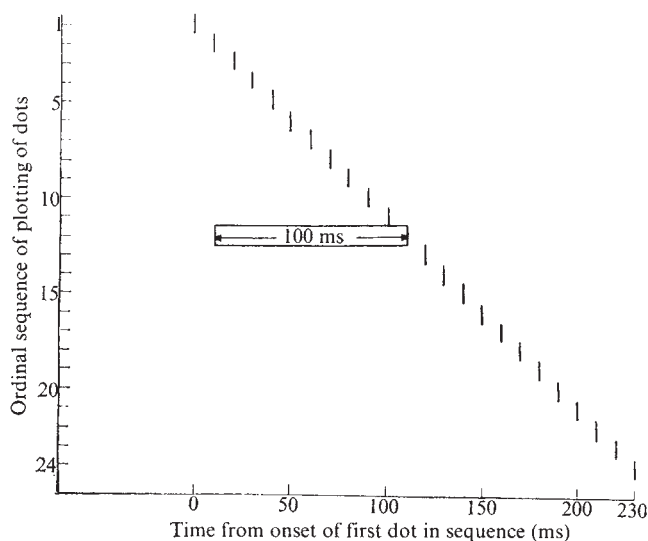


Fig. 3 Temporal distribution of errors in the results of the second experiment. Within each graph, the abscissa indicates the ordinal position of each dot within the plotting sequence, irrespective of spatial location; the ordinate shows the proportion of trials on which a dot plotted in the indicated ordinal position was incorrectly identified as missing. \circ , Control condition where every dot was plotted for 1.5 μ s; \bullet , experimental condition where all dots were plotted for 1.5 μ s except the 12th dot which was plotted for 100 ms. *a*, Subject L.D.C.; *b* V.D.L.

observer. Clearly, the probability of erroneously identifying the 12th dot in the sequence as missing was distinctly higher when its physical duration was long than when it was brief. Similar results were obtained with several other observers.

Unlike the first experiment, where perceptual segregation of the two portions of the display might have been possible, the continuous distribution of the dots over the entire plotting interval made segregation an all but irrelevant consideration in the second experiment. The results also deny the possibility that the termination of the 12th dot might have triggered some sort of discontinuity-detection mechanism within the visual system: had this been so, all dots plotted before the termination of the 12th dot would have become perceptually segregated from the remaining dots. On the contrary, the error distribution (Fig. 3) shows that the dots closely preceding or following the 12th dot in the display sequence were confused with the missing dot much less frequently than the 12th dot.

Contrary to most current thinking^{1-4,9} where iconic memory is said to begin at the termination of a display and to fade rapidly thereafter, the present findings suggest that

iconic memory (as distinct from a retinal after-image) begins at the onset of a display and continues only for a given duration (see also refs 10–13). Thus, iconic memory remains available after the termination of a display only if the duration of the inducing stimulus does not outstrip a given maximum duration from the onset of stimulation. This pattern of results strongly suggests that iconic memory may be more properly viewed as the product of neural processes of finite duration rather than as a sensory store whose contents begin to fade when stimulation terminates. The nature of the processes cannot yet be identified, but there is some support for the view that sensory persistence is produced by the activity of coding mechanisms at the level of feature extraction in visual information processing¹⁴. On this view, persistence would continue while the coding mechanisms are active and would cease at the termination of that processing phase, whether or not the inducing stimulus is still on display.

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Cuckoo among Lake Malawi cichlid fish

THE family Cichlidae consists of bony, perch-like fish which are found in many of the fresh waters of America, Africa and Asia. In Africa most of the almost 700 species occur in the Great Lakes. Approximately 300 species are known in Lake Malawi and 98% of them are endemic to it. Like cichlids from elsewhere, they have intricate but stereotyped territorial and courtship behaviour, followed by spawning and a period of parental care¹. Substrate spawners lay their eggs on the substratum or a suitable object and both parents guard the eggs and later the developing fry^{1,2}. In Lake Malawi the only known substrate spawner is *Tilapia rendalli* Dumeril, a non-endemic species. Evidence suggests that all other cichlids of Lake Malawi are maternal mouthbrooders. When eggs are laid they are picked up by the females and brooded in the mouth^{1,2}. When fry are ready to emerge the parent releases them at a suitable site and usually remains to guard her brood, recalling them into her mouth in the event of danger^{1,2}. After several days, fry no longer respond to their mother's recall signals and the association is terminated. Although cichlid parents usually guard their fry ferociously it seems that at least one species passes these parental duties on to other species of cichlid.

In May 1976, during diving off Likoma and Chisumulu Islands (Lake Malawi), maternal *Haplochromis polystigma* Regan were found caring for mixed broods: their own offspring, easily recognised because they have adult coloration and markings from the outset, and fry of another species differing slightly in size and markedly in coloration. *Haplo-*

chromis macrostoma Regan and *Serranochromis robustus* Regan were also found guarding mixed broods. The foreign fry appeared to belong in all cases to a single species, and differed sufficiently from the native fry to be readily distinguished. When prompted by divers, the guarding parents always retrieved their mixed broods. On occasion, they collected their own fry with greater facility than the foreign individuals, possibly due to a better response of their own progeny to recall signals.

As mixed broods were found on several occasions with each of the three parental species it is unlikely that foreign fry were included by chance. During the 10-d period at Likoma and Chisumulu Islands, *H. polystigma*, *H. macrostoma* and *S. robustus* parents were not found with pure broods.

Members of a mixed brood of *S. robustus* were caught and reared and the cuckoo was identified in January 1977 as *Haplochromis chrysonotus* Boulenger. *H. chrysonotus* is widespread in Lake Malawi and is a member of the Utaka group, which are plankton feeders³.

When the observations were made, shoals of *H. chrysonotus* brooding eggs or fry in their mouths were common in the surface waters. Surrogate parents were found beneath them on the rocks in 2–10 m depth. How the transfer of fry from *H. chrysonotus* to the foster parents takes place is unknown. The three species of foster parent are all active predators and it is conceivable that *H. chrysonotus* forms part of their diet.

It is easy to understand why *H. chrysonotus* progeny should accept foster parents because fry of maternal mouthbrooding cichlids show a very poor parental recognition response. They will follow and attempt to enter crude models which bear no resemblance to the parent in colour, shape, size or markings^{1,4}. Virtually all that is required to induce following is for the model to be moved in a manner which simulates calling behaviour.

It is not easy to understand why foster parents accept and care for fry markedly different from their own. Laboratory experiments^{5,6} with substrate-spawning cichlids have shown that broods could be swapped or mixed provided the progeny were very similar in age, size and behaviour. Dissimilarity of one or more of these criteria invariably resulted in the foster parent eating the foreign fry. Clearly the success of a cichlid cuckoo depends on accurate timing of introductions to the native brood and a similarity of behaviour. Furthermore, provided *H. chrysonotus* fry become intermingled in the foster parents' brood, then even if the parent were reluctant to accept them she would be unable to remove them. A predatory approach towards a mixed brood would evoke an avoidance reaction in all its members. In such circumstances foreign fry would be protected from the surrogate mother by shoaling with her own fry, and protected from other predators by their foster parent when they are taken into her mouth.

Cichlid fry reared with foster parents have been found to prefer the foster parental species to conspecific mates when placed in choice chambers at sexual maturity⁷. In natural conditions, however, *H. chrysonotus* and the three species of foster parent apparently breed true. It is therefore improbable that foster parents become imprinted on *H. chrysonotus* fry to such an extent as to impair subsequent recognition of conspecific rivals and mates.

Although *H. chrysonotus* brood their own eggs in their mouths, they are cuckoos in the sense that foster parents guard their young. This observation raises questions concerning the significance of the parent-brood relationship, the behavioural mechanism(s) of brood hybridisation, and the role of *H. chrysonotus* as a parent.

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