THE EFFECT OF THE SPACING OF BACKGROUND ELEMENTS UPON OPTOMOTOR MEMORY RESPONSES IN THE CRAB: THE INFLUENCE OF ADDING OR DELETING FEATURES DURING DARKNESS

BY RICHARD HIRSH* AND C. A. G. WIERSMA

*Division of Biology, California Institute of Technology,
Pasadena, California, U.S.A. 91125*

SUMMARY

1. Study was made of the effect of separation between stripes in the visual field upon responses which indicate memory of those stripes.

2. The amount of separation between white stripes had very little effect, whereas response strength and the amount of separation between black stripes were directly proportional.

3. The presence of extra, non-displaced black stripes prior to or following displacement reduced the size of the memory responses.

4. The effects of the amount of separation in the two cases were comparable. In both situations the separation affected only the responses to displacement of the stripe borders nearest to the extra stripe.

5. The effect of extra stripes present prior to displacement was in turn affected by the duration of the dark period, whilst the effect of those present during the post-displacement period was not. This accounts for the larger effect of extra stripes present during the post-displacement period.

6. By expanding stripe width during darkness it was possible to distinguish between the effects of distance between stripes and the amount of white space separating them. Reducing white space while distance remains constant causes reductions in response strength, whereas reducing the distance between a memory zone and the white space between it and the neighbouring stripe increased the size of the memory response.

INTRODUCTION

It has been demonstrated that memory is a feature of the optomotor systems of some decapod crustaceans (Horridge, 1966*a*; Wiersma & Hirsh, 1974) and an insect (Horridge, 1966*b*). In such experiments the animal is placed in a stationary visual surround, usually consisting of vertical black and white stripes. After a period of viewing the surround is angularly displaced in the horizontal plane unseen in darkness. Upon re-illumination the animal redirects its gaze, to resume the previous orientation to the background. Since it has been shown that this response is not due to the maintenance of a fixation upon some aspect of the background (Wiersma & Hirsh, 1975*b*) it can be concluded that the animal has remembered its pre-darkness orientation to the

* Present address: Department of Psychology, McGill University, Montreal, Canada.

background and is responding to the difference between that orientaton and the newly visible one. In the present study upon *Pachygrapsus crassipes*, we have employed spike frequency in the optomotor neurones as an indicator of the memory response, as in previous studies (Wiersma & Hirsh, 1974, 1975*a*, *b*).

When stripes form the background, optomotor spike frequency in *Pachygrapsus* is directly proportional to the number of stripes present in the visual field when the separation between stripes of the same colour is kept constant (Wiersma & Hirsh, 1975*a*). This indicates that the stripes are individually remembered. Further the stripes are remembered in terms of their position upon the retina. Interaction between a visible and a remembered stripe occurs only when the images of both have fallen on the same local region of the retina (Wiersma & Hirsh, 1975*a*). These latter conclusions were reached in studies employing a block of four black and three white stripes all 12° wide so as to yield a pattern with a period of 24°. This pattern was angularly displaced 27° in the direction in which the motor fibre under observation caused the eye to move, or 21° in the opposite direction. Displacement in this latter direction causes inhibitory responses in most circumstances. The resulting responses were then compared. After a 27° displacement the lead stripe is quite far away from any former stripe position but each of the other three black stripes is no more than 3° away from a former position of a black stripe. After the 21° displacement the lead stripe is greatly removed in the inhibitory direction from any former stripe position. Each of the other three stripes due to the periodicity of the pattern, is again 3° away from a former stripe position in the excitatory direction. If the memory response results from a comparison between the positions of the stripes with respect to some fixed external reference before and after movement, then in one case the response should be excitatory while in the other it should be inhibitory. However, if each local region of the eye serves as its own reference the two situations are more similar than dissimilar. Not only were the responses in both cases excitatory but they also consisted of equal frequencies, indicating that no interaction occurs when the positions of visible and remembered stripes are widely separated.

A stripe may be considered as a set of two borders. With the aid of an apparatus that allows the borders on the left sides of stripes to be moved while those to the right remain stationary, or vice versa, it has been shown that the position of each border is remembered individually by *Pachygrapsus* and that the response to stripe movement consists of the sum of responses to border displacement (Wiersma & Hirsh, 1975*b*).

The above observations can be accounted for by a theory postulating that memory zones form in the optic system of *Pachygrapsus* at sites where visual contrast is present. According to this theory, when vertical black and white stripes are present in the visual field, a black-sensitive zone develops on the white side of each border in the optic system and a white-sensitive zone develops on the black side in a process similar to lateral inhibition as seen in the lateral eye of *Limulus*. The memory zones respond to those decreases or increases in the intensity of light falling upon them which result from background displacement. Activation of zones to the left of vertical borders causes excitation of the motor fibres responsible for leftward movement and causes inhibition of their antagonists. The opposite is true for zones located on the right sides of vertical borders. It has also been shown that activation of white-sensitive zones causes weaker responses than activation of black-sensitive zones, and that the effect of

activation is greatest near the original border location and is weaker from zone parts further removed from it (Wiersma & Hirsh, 1975 *b*).

A memory zone in *Pachygrapsus* subsumes approximately 4° (Wiersma & Hirsh, 1975 *b*). With this value, the above theory has been used to make predictions about the shape of the function relating the size of the memory response to the angle of background displacement, and the predictions have been tested and verified for single borders, sets of borders of one kind, black and white stripes of equal width, with regular patterns in which the white stripes were wider than the black ones (Wiersma & Hirsh, 1975 *b*). The theory makes rather exacting quantitative predictions about the relationship between response size and displacement when single black or white stripes are used. These, too, have been confirmed (Wiersma & Hirsh, 1975 *b*).

However, it has also been found that changes in light intensity in the memory zones are not the only factor affecting the memory response in *Pachygrapsus*. When two black stripes fairly close together are turned in the dark, the resulting response can be up to 50 % less than that when the two are separated by a larger distance (Wiersma & Hirsh, 1975 *a*). Here this will be called the spacing effect.

One aspect of the spacing effect is that removing one or two stripes from the centre of a block of stripes does not cause a marked reduction of the size of the memory response, though when they are added at the edges of the block the response grows linearly. It might be thought from this that only the outer stripes of a given block would contribute to the memory, but that this is not so was shown by moving only inner stripes during darkness, leaving the outer stripes in place. This stratagem yielded relatively small but clear memory responses (Wiersma & Hirsh, 1975 *a*).

The size of the memory response as a function of the displacement in darkness is not affected by spacing. The ratio of the responses to various displacements within the limits of the memory zones remains the same, no matter what the spacing of the stripes, when periodically patterned stripes of the same width are used (Wiersma & Hirsh, 1975 *b*).

The following experiments were done to further explore the nature of the spacing effect. The experiments required that the space around given zones could be altered without actually interfering with the zones themselves. One of the simplest ways of accomplishing this is to have some stripes present, at different distances from the ones to be displaced, only during the viewing period prior to displacement. Initially we intended to explore only such pre-displacement effects as it was thought that spacing operated solely upon the strength of the developing memory zones. However, since during the viewing period following displacement extra stripes could be presented as readily as during the pre-displacement period this situation was also studied. To our surprise the effects were even greater. Thus it became important to compare the results in analogous pre- and post-displacement situations.

METHODS

Recordings were made of the discharge rates of single motor neurones responsible for horizontal eye movements in the shore crab, *Pachygrapsus crassipes* (Randall). Maintenance of these animals and the recording techniques employed were as described previously (Wiersma & Hirsh, 1974).

A few experiments were done with the animal in a rotatable drum, but in most the

animal was suspended in the centre of a stationary drum (17 in high and 16 in in diameter) with an opening 14 in high and 119° wide cut in its wall.* On each side of the opening a door of the same dimensions as the opening was mounted. Cue cards were detachably mounted inside the doors. Different cards were presented to the crab by opening one door and shutting the other, during darkness. The inside of the drum and the inner face of each door were painted white. To mimic displacement of black vertical stripes, use was made of two cue cards, differing in stripe position by 3°. Either right or left stripe displacements were simulated. By using different sets of cue cards, the number and pattern of the stripes could be altered within limits set by the width of the doors. With this set-up it was also possible to alter the stripe pattern presented before and after darkness by adding or removing stripes on the second door. The additional stripes were added as thin metal strips. Numerous small magnets on the outside of the door fixed the strips by magnetic attraction.

As in past experiments a standardization procedure was often employed to overcome the effect upon the results of the variability in firing frequency that was found both within a single experiment and between animals. Background firing rates at the start of the experiments ranged between 12 and 34 Hz, and could vary rapidly by factors ranging from 1·1 to 2·9. Seventy per cent of the animals showed changes by a factor of at least 2 at least once during an experiment. Since firing rates during responses definitely varied with background rates, counts of the number of spikes constituting a response were often inadequate for comparative purposes.

In the standardization procedure, the response to a standard pattern was measured. The standard pattern consisted of two stripes separated by distances from 48° to 155°, depending upon the experiment. The separation was chosen to produce the maximum possible response to the standard under the experimental conditions. Trials were alternated, with 3° displacements of either the standard or a test pattern. The test responses as a rule were smaller than standard ones due to the experimental manipulations. Thus the results were expressed as a percent reduction from the mean of the preceding and the following standard responses. This value was calculated according to the formula:

$$\text{per cent reduction} = \frac{\bar{S} - T}{\bar{S}} \times 100,$$

where $\bar{S}$ is the mean of the two standard responses and T is the test response.

It should be noted that the definition of the response in the first experiments to be reported is different from those in following experiments. The first experiments involve the effect of the separation between two white stripes on a black background. So that these results would be comparable to previously published ones for black stripes (Wiersma & Hirsh, 1974), the response was defined as the difference between the number of action potentials occuring in the first 5 s after re-illumination following a positive displacement and that following a negative one. However, in subsequent experiments the variation in the negative response due to experimental manipulations was so small as to preclude usefulness. Hence only the responses to positive displacement, the number of action potentials occurring in the 5 s immediately after re-illumination minus that for the 5 s immediately prior to the dark period, were computed.

* Designed and constructed by Ken Hollis.

RESULTS

Effect of black space between white stripes

The spacing effect was originally found (Wiersma & Hirsh, 1975*a*) by changing the distance between black stripes of a given width by various amounts. In the present study, investigation was made of whether or not a similar separation of white stripes would give equivalent results. With the rotatable drum, displacements were made of two white stripes of 12° separated by either 12° or 48°. For 3° displacements of the 12° spaced white stripes responses were $8 \pm 5\%$ smaller than those for the white stripes separated by 48°. This reduction is significant ($t = 3.85$, $P < 0.01$) but small compared to that obtained for black stripes (see Fig. 2; Wiersma & Hirsh, 1975*a*). In some cases it was possible to show for the crabs used here that this was indeed the case, but because this required extensive changes in the experimental set-up which disturbed the animals it was not possible to do it for all preparations. The effect of white-stripe spacing was so small that it did not seem to warrant further investigation, and therefore all following experiments deal only with white space between black stripes.

Properties of the spacing effect

When extra stripes were presented only prior to displacement, a clear reduction in response size resulted. The responses to displacing a standard pattern of two 6° black stripes separated by 79° were compared to those when four additional stripes were present prior to displacement. These extra stripes were separated by approximately 11°, as illustrated in Fig. 1. Although the absence of the extra stripes following displacement would, as the figure shows still cause their white-sensitive memory zones to be activated, no net contribution to the memory response ensued because the number of positive and negative zones was equal, and therefore cancel each other's effects.

The results obtained with a dark period of 10 s duration are presented in Table 1A. The mean reduction was $43 \pm 21\%$ of standard. Similar results were obtained from animals with eyes glued in place, thus excluding the possibility that the effect was due to changes in eye position during darkness. When, during the pre-displacement period only, two additional stripes separated by approximately 22° from the two stripes of the standard pattern were presented, the mean reduction was $28 \pm 6\%$, and thus significantly smaller than in the case of the four extra stripes.

It was found that it is not the number of extra stripes as such, but their nearness to the ones to be displaced, which is the significant factor leading to the above reduction. Thus when a single extra stripe was placed midway between the two standard stripes only slight effects were observed, whereas definite reductions occurred when this extra stripe was placed close to one or the other standard stripe. By placing additional stripes either in front of or behind the two standard stripes, investigation was made of whether a neighbouring extra stripe affects zones at both borders of a displaced stripe or only those nearest to it. The standard pattern consisted of two 6° stripes, separated by 60°. During the viewing period prior to displacement two additional 6° stripes were placed both 12° in front of, or both 12° behind, the standard ones. These two conditions were presented to all five animals used in this series. As illustrated in Fig. 2, for
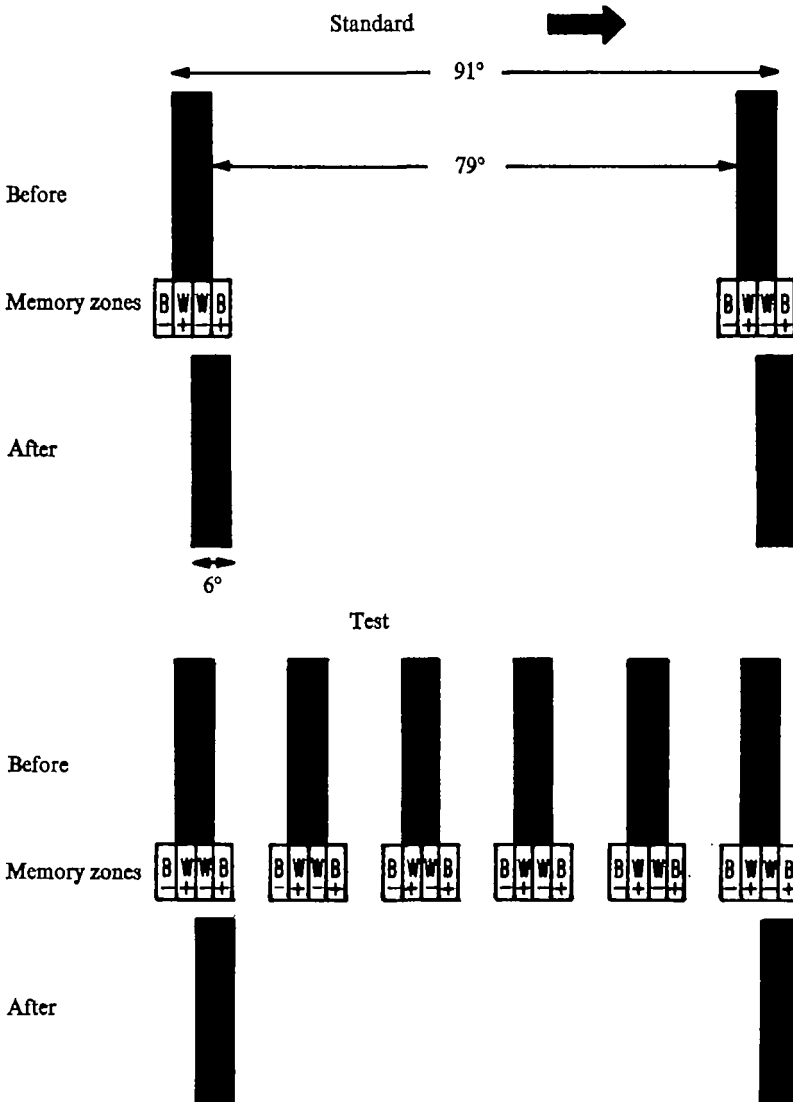
Fig. 1. Schematic representation of the experimental set-up for investigating the effect of close spacing when present during pre-displacement period alone. The arrow indicates the direction of positive displacement. 'Before' designates the pattern present prior to the dark period, and simulated displacement, while 'After' denotes the one present on re-illumination, as in following figures. The responses to the test situation compared to those to the standard one are given in Table 1.

one of the two standard stripes, an additional stripe placed in front of a standard stripe is closest to a positive black-sensitive zone, while one placed behind the standard stripe is nearest to a positive white-sensitive zone. As stated above, white-sensitive zones are known to be only half as effective as black sensitive ones (Wiersma & Hirsh, 1975b). If the extra stripes affect only the memory zones nearest to them, the reduction caused by those behind the standard stripe should be half of that caused by those placed in front of the standard stripes. The data are presented in Table 2. The stripes in front caused a mean reduction of $26 \pm 14\%$, whereas this value was $13 \pm 4\%$ for those behind.

Table 1. *Reductions as percentages of standard response strength caused by extra stripes present during (A) the pre- or (B) post-displacement period alone*

Crab	A	B
1	24	94
2	52	72
3	31	99
4	17	48
5	70	84
6	74	107*
7	36	27

* This fibre was more active after negative displacements than it was in response to the positive ones.
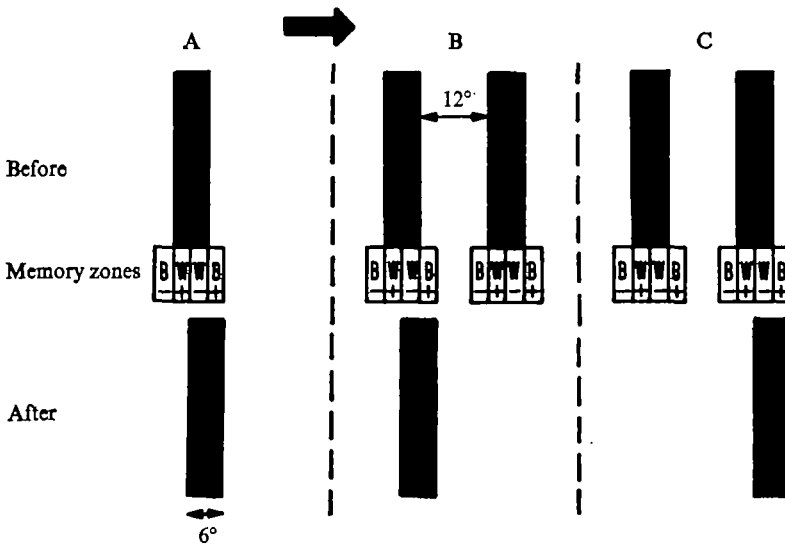

Fig. 2. Schematic representation of the experiments in which extra stripes were present during the pre-displacement viewing period, either in the direction of subsequent stripe movement, or on the opposite side. In each case only one of the two standard stripes and its extra stripe are shown. The distance between the two standard stripes was 60°. The boxes below the stripes represent the memory zones caused by the stripe borders. B zones are black sensitive, W zones are sensitive to whiteness. +zones excite and −zones inhibit the fibre studied. A, standard; B, leading extra stripe; C, trailing extra stripe. The results are presented in Table 2.

These two sets of reductions are significantly different ($t = 2.84$, $P < 0.05$). Therefore it is likely that only the nearby memory zones are influenced by the presence of the extra stripes. Further, the effect of an extra stripe is blocked when another one is closer to the standard stripe. This was shown as follows. In the standard trials each of two 6° stripes separated by 65° had an extra stripe about 9° in front of it during the first viewing period. This is shown for one of the two standard stripes in Fig. 3A. Two test conditions were compared. In the first an additional extra stripe was placed 24° behind each standard stripe (see Fig. 3B); in the other the additional extra stripes were placed 24° in front of the standard ones. As Table 3 shows, the reduction in the first test condition was greater than in the standard trials, whereas no additional reduction was obtained in the second test condition.

Table 2. *Reductions as percentages of standard response strength caused by extra stripes nearest black- or white-sensitive zones present prior to displacement*

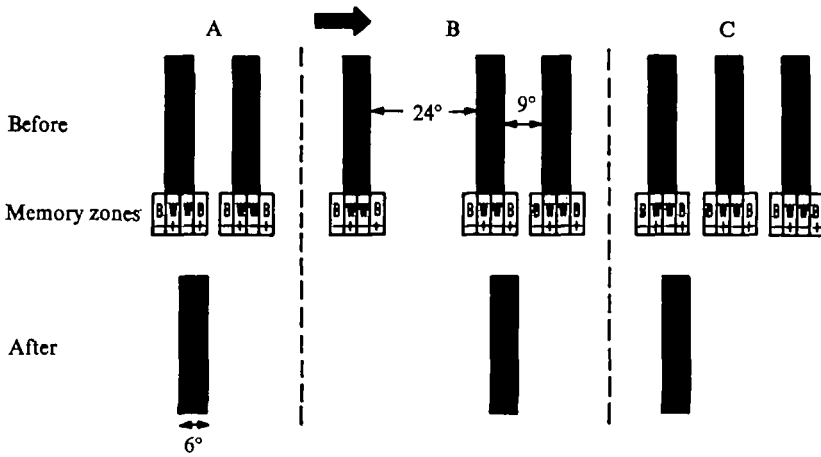| Crab	B zone	W zone
A	52	22
B	24	13
C	8	18
D	27	15
E	19	18
F	20	6
G	20	9
H	42	12

Fig. 3. Schematic, of the experiments showing that an extra stripe is effective only when it neighbours the standard, displaced stripes. As in Fig. 2 only one standard stripe with its extra stripes is drawn. A, standard, in which one extra stripe is present during the pre-displacement period. B, during the pre-displacement period the standard is flanked by an additional extra stripe C, the second extra stripe is placed at the same distance of the trailing one in B, but now on the leading side. As seen from Table 3 this prevents it having an influence on the strength of the memory response.

Table 3. *Comparison of (B), the effects of immediately neighbouring and of (C), non-neighbouring extra stripes, present during the pre-displacement period. The responses are presented as percentages of those when only one extra stripe was present (condition A of Fig. 3)*

Crab	B	C
a	31	83
b	93	116
c	33	110
d	55	70
e	85	120
f	93	100
g	96	130
Mean	69	104

Table 4. *Comparing the effect of distance on the mean percent reduction from standard in the pre- and post-displacement situations*

Distance ...	11°	22°	Ratio
Read-in	43±21	28±6	0·65
Read-out	76±27	50±6	0·66

Post-displacement effects

As stated above, when closer spacing is present during post-displacement period only, by the addition of extra stripes during the dark period, the memory responses are also reduced. This is contrary to what might be expected from simple zone theory alone. When four additional stripes were placed between the two stripes on the post displacement cue card, in positions corresponding to those used in the experiments on pre-displacement spacing (Fig. 1), significantly larger reductions were obtained, as shown in Table 1 B. As can be seen from this table, there were practically no responses at all to the 3° displacements of the standard stripes in about half of the experiments. The mean reduction was $76 \pm 27 \%$. Compared to the reductions obtained in the pre-displacement experiments the effects were significantly greater ($U = 9, P < 0.05$)

The question whether the process underlying the reduction in the post-displacement situation was the same as that responsible for the pre-displacement reduction arose immediately. The previously described experiments were repeated with close spacing present only following displacement. As with extra pre-displacement stripes only neighbouring stripes were found to exercise an influence and such stripes affected zones only at borders nearest themselves. The data for the latter finding were less variable in the post-displacement situation than when close spacing was presented prior to displacement, which was shown in Table 3, condition B. As in the pre-displacement experiments, glueing the eyes was inconsequential.

The absolute values for the post-displacement reductions are always greater than for the pre-displacement ones, and this is especially evident for close spacings. However, this does not necessarily indicate that the effect of distance is different in the two cases. Suppose that a factor independent of distance were acting as a multiplicative constant in the post-displacement situation but not in the pre-displacement one, then the absolute values would be different even though the effective range of distances were the same. To control for such a factor, it is necessary to normalize the two situations; that is to compare the influence of different distances in each situation separately before making a cross-situational comparison. To this end additional stripes were placed between the standard ones so that they were separated from them by 22° or 11° prior to or following displacement. As can be seen in Table 4 the ratios of the sizes of the responses for the two separations is the same in both situations, proving that the influence of distance is the same in both cases.

The difference between pre- and post-displacement reductions

The pre-displacement reduction must necessarily be mediated by memory in some form since the extra stripes are not present during production of the memory response. Like the memory zones it may therefore be subject to forgetting and decline during dark periods. On the other hand, the post-displacement spacing effect is obviously not
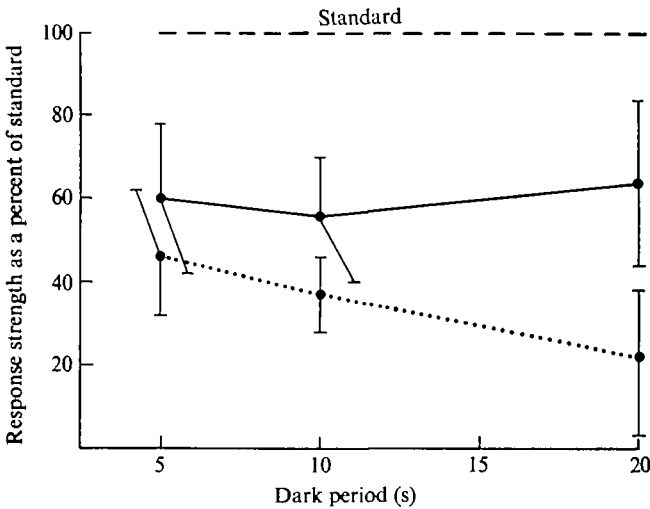
Fig. 4. Response strength as a percent of standard when close spacing is present during the pre- or post-displacement period plotted as a function of the length of the dark period. The difference between the standard line and the plotted lines represents the reduction as a percent of standard.

dependent on memory and thus cannot be affected by the length of the dark period.

To test the possibility that forgetting is responsible for the pre-displacement reduction being smaller than the post-displacement one, four additional stripes were presented only before or after displacement in trials where the dark period was either 5, 10, or 20 s. Standard trials were run separately for each dark interval. With this procedure it is possible to cancel the effects of the decline in strength of the memory zones by arbitrarily setting the standard response in each of the three conditions to 1. This allowed the use of data from preparations in which it was not possible to get values for all three conditions. The results are presented in Fig. 4. Note that when close spacing is present prior to displacement only the reductions are a constant percentage of the standards, indicating that the memory factor mediating the pre-displacement effect declines in the dark at the same rate as the memory zones. When extra stripes are present during the post-displacement period the absolute size of the reduction is constant, while the size of the standard declines with time. Thus as the dark period lengthens the response becomes a decreasing proportion of the standard.

White space and distance

One question of interest is whether the spacing effect is determined by the white space between a zone and the nearest neighbouring stripe or the distance between them which would be the case if the neighbouring stripe were exerting a negative influence upon the zone. In the preceding experiments the two factors, white space and distance, were always identical. However, in the context of post-displacement effect it is possible to separate these factors. The white space between a zone and the nearest stripe may be varied while the distance between them remains constant by moving the stripe border considerably beyond the zone as shown in Fig. 5 B.
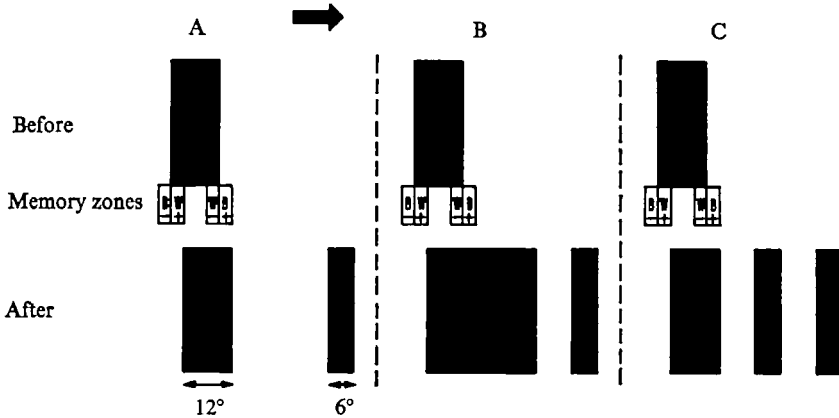
Fig. 5. Schematic representation of the experiments for testing the separate effects of white space and distance. A, one half of the standard patterns presented during the pre- and post-displacement periods. As in B and C the patterns were repeated so that corresponding stripes were separated by 70°. B, during the post-displacement period the white space between the original positon of the displaced border and the nearest extra stripe is reduced, but the distance between the memory zone and the extra stripe is as in A (see Table 5). C, by placement of an extra black stripe, the white space between the original border and the nearest stripe during the post-displacement period is the same as in condition B but is closer to the memory zone (see Table 6).

Table 5. *Percent reduction in response strength when the white space between zones and neighbouring stripes is reduced from 27° to 9° while distance between them remains constant*

Crab	% reduction
I	31
II	17
III	18
IV	11
V	7

This was done in an experiment in which a pattern of two 12° stripes separated by 70° were displaced 3°. Upon re-illumination in the standard condition an additional 6° stripe appeared 27° in front of each of the displaced ones (Fig. 5A). In test condition B the front border of each stripe moved not 3° but almost 19°, leaving only approximately 9° of white space. Standard and test condition trials were alternated three times. The dark period was 8 s. Reducing the white space caused reductions in the response size (Table 5.)

It is also possible to do the converse experiment, of varying distance while white space remains constant, by inserting one more additional stripe into the standard post-displacement pattern approximately 9° in front of each of the two displaced ones (Fig. 5C). The white space is then the same as that in condition B but the distance from the zone of that space (and of course to the neighbouring stripe) is much less. Conditions B and C trials were alternated three times. When the white space was was closer to activated zones responses were larger (Table 6). Note that if the neighbouring stripes had been exerting a negative influence the opposite would be true.

One possibility is that the more distant white space is less effective because it is separated from the activated zone by a black area and not that it is simply more

Table 6. *A comparison of memory responses expressed in increased number of spikes when the distance between a constant area of white space and the activated zones is varied*

Crab	Near	Far	Difference
α	77	34	43
β	94	26	68
γ	119	55	64
δ	57	39	18
ϵ	70	45	25

distant. To test this possibility the effect of thin ($1.25°$ wide) and thick ($15°$ wide) additional stripes placed in front of the two displaced stripes in the post-displaement pattern were compared. The displaced stripes were $70°$ apart so that the additional stripes between the displaced ones did not affect the zones at the rear of the displaced stripe in front of it. No consistent difference between responses in these two condition was observed.

DISCUSSION

When the present series of experiments was begun, it was thought that as the separation between stripes were to be decreased, there would be a decline in the sensitivity of the memory zones formed. The spacing effect would then be completely due to factors present during zone formation prior to displacement. The processes involved would thus be analogous to those responsible for the formation of the zones themselves (which are similar to those involved in lateral inhibition) and rather easily analysable. As it turned out, the situation is much more complex, and as yet we cannot offer a hypothesis which encompasses all the results.

The greatest surprise was that post-displacement spacing was as important (if not more so) in determining the memory response as the spacing present prior to displacement. Since the memory zones are highly local, zone theory predicts that the addition of stripes relatively far from them during production of the memory response would be without effect. It has been observed that when a border is moved so that it passes over the zone even for a considerable distance, the memory response generated does not differ from that to a lesser displacement which also completely activates the zone (Wiersma & Hirsh, 1975b). However, in the present experiments, introducing extra stripes during the dark period had a definite influence even though they did not overlap memory zones. Furthermore, the factors governing the reduction caused by extra stripes in the pre- and the post-displacement situations were the same. The sole exception was that close spacing following displacement was more effective, presumably because it is not subject to forgetting during darkness. By the same token the extra stripes present following displacement cannot have influenced the strength of the memory zones.

Whether pre-displacement spacing affects the memory zones as such or is due to a separate memory mechanism was examined by combining pre- and post-displacement spacing of various types in unreported experiments. Unfortunately, the results were equivocal, so that this question could not be answered.

Attempts to elucidate the factors responsible for the spacing effect were more successful. As a working hypothesis, it was supposed that the formation of new memory

zones might, in some way, interfere with the expression of existing ones and that the closer these new zones were to the old ones, the greater the inhibitory effect would be. Obviously, this asked that only new borders facing the displaced ones would have spacing influence; otherwise the generation of new memory zones resulting from normal displacements, uncomplicated by extra stripes, would eliminate memory responses. The fact that an extra stripe placed in front of the displaced one is more effective than one placed behind it shows that in the first instance the black-sensitive positive zone is involved, whereas in the second case it is the white-sensitive positive zone that is less completely activated. This finding indicates that only new edges immediately adjacent to the ones contributing to the memory response are involved in the reductive effect. The same conclusion is reached by the findings that additional extra stripes separated by another new one from the nearest memory zone never contribute to the amount of reduction obtained by the nearest one alone.

Whereas the hypothesis thus was in agreement with a number of experiments, it failed completely to explain why a memory response obtained from a memory zone quite far away from newly forming ones could be greatly reduced (see Table 6).

A more close relationship appears to exist between the amount of white space and the strength of the memory response. If this amount is small a weak response will ensue; when it is larger the response increases in strength. This would indicate that in some way the response of black-sensitive zones is driven by the white area bordering it. White-sensitive zones may perhaps be similarly influenced by the size of black areas, but the effect would be expected to be weaker, because of the fact that white-sensitive zones contribute only half as much as black-sensitive ones to the memory response. It is, however, not clear what fundamental mechanism would cause the direct relationship between the amount of white space and the strength of the memory response.

A further disturbing observation is that the distance from a black-sensitive memory zone to a bordering white area appears to have an influence on response strength, in that a white area of a given size gives a stronger response when the memory zone is located close to it than when it is far away. From a number of previous experiments, one would expect that this factor would not have played a role (e.g. Fig. 7, Wiersma & Hirsh, 1975 b). It will be necessary to retest these situations before it can be definitely concluded that the effect of white space diminishes with the distance it has to travel to cause a memory response.

Another unsolved question is what prevents the influence of a large white space from crossing extra black stripes as thin as $1 \cdot 25°$. Further experimentation with even thinner stripes is necessary in this and other respects.

The spacing effect can be regarded as a means by which the proportionality between displacement and the ensuing eye movement is more or less maintained regardless of the structure of the background. As was shown previously, memory responses increase in strength with number of stripes present, but this effect is greatly compensated by that of spacing. For the same reasons it is strongly indicated that the same factors would play a role in optokinetic reactions. Otherwise, under natural conditions, a finely structured background would cause much larger eye movements than one with only few contrasting regions.

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