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Visual Pattern Discrimination in a Butterfly

A Behavioral Study on the Australian Lurcher, *Yoma sabina*

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Numerous studies on pattern recognition in insects have shown that shape parameters play a role in a variety of visual tasks (for review see [1]). Studies on various butterfly species have shown, for example, that recognition of potential mates is based on the pattern displayed on the butterfly's wings [2], although color and motion cues are thought to be of more widespread significance [3]. The present behavioral study, using moving dummy butterflies, investigates spontaneous pattern preferences in the Australian lurcher butterfly, *Yoma sabina* (Nymphalidae). The results show that several parameters of the species-specific wing pattern are innately attractive to this butterfly. Thus, the wing pattern might play a role in mediating interactions among conspecifics.

The experiments were performed from June 1994 to March 1995 in Canberra with males of the Australian lurcher, *Yoma sabina* (Nymphalidae) [4]. This species was selected for various reasons. As a tropical butterfly, the lurcher does not diapause and can be bred during the whole year. It is large,

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and thus likely to be accessible to investigations at the neuronal level. Most important, it possesses a distinct wing pattern. Its most conspicuous feature is the broad orange band on the dorsal wing surface of its fore- and hindwings (Fig. 1 A). The rest of the dorsal wing surface is dark brown, except for small dots that differ between the sexes, being orange in males and white in females. The ventral wing surface is quite cryptic with a brownish tint. Pupae of the lurcher were purchased from a butterfly farm (Mount Glorious Biological Centre, Queensland, Australia). After hatching, the butterflies were kept in a greenhouse (floor area $2.5 \times 2.5\ m^2$, height between 1.6 and 2.2 m) where they could fly freely. The temperature in the greenhouse was regulated such that it did not increase above 35 °C on sunny days and did not fall below 15 °C even in cold nights. The butterflies were fed with a honey solution which covered the bottom of a small Petri dish. Usually, between 10 and 20 male butterflies and up to 5 females were kept simultaneously in the greenhouse. The females were marked with paint on their ventral wing surface to enable the observer to differentiate easily between male and female butterflies. The butterfly dummies were made of black and orange cardboard (see insets of Fig. 1 B–F). Since preliminary observations revealed that the lurcher does not approach stationary dummies that resemble conspecifics, the butterfly dummies were moved in a height of about 1.5 m, using a commercial gadget ("Original Fluttering Budderfly", Martin Paul Inc., Denton, Texas, USA). The dummies were attached to a bent wire that was connected to a rotating wheel. The dummy performed erratic movements that vaguely resembled the movements of a real butterfly. The dummies were inclined with respect to the horizontal by about 45°. In all experiments, two dummies were presented simultaneously 60 to 70 cm apart.

Australian lurchers approach the moving butterfly dummies in a way similar to that in which they approach conspecifics. When sitting on a twig or when flying around, they suddenly accelerate and start following another animal or one of the dummies. Such an encounter may last for several seconds. The distance to another animal or to a dummy may decrease to only a few centimeters. By counting the approaches to each of a pair of simultaneously presented dummies, it was determined whether the lurcher spontaneously prefers one dummy over the other. After 20 approaches, the positions of the two dummies were interchanged to exclude the possibility that the but-

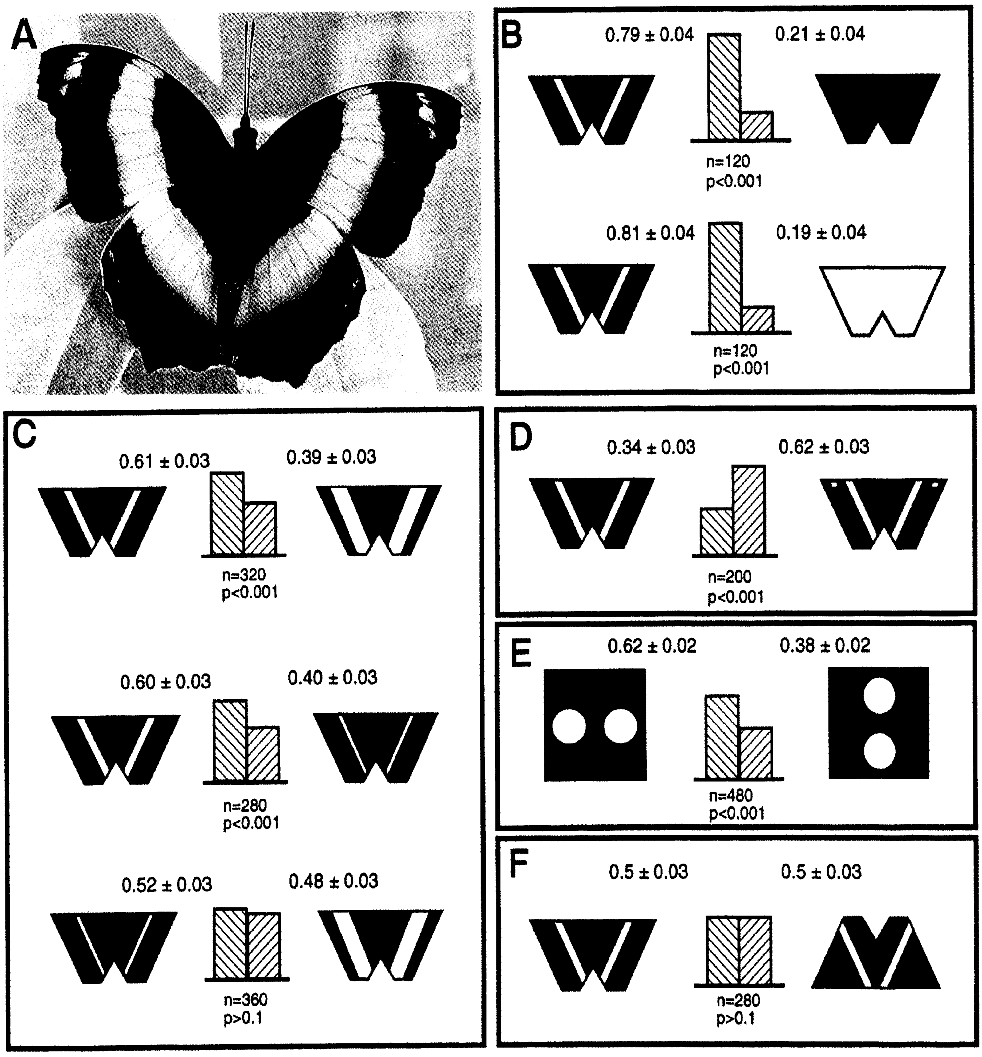

Fig. 1. A) Male Australian lurcher, *Yoma sabina* (dorsal view). The wings are dark brown except for the broad median stripe on each fore- and hindwing and the small dot on the apical part of each forewing that are orange. The wing span, i.e., the distance between the outstretched forewings, of the lurcher is approximately 80 mm. B–F) Responses to various pairs of dummy butterflies made of black and orange cardboard (see *insets*). Size of the dummies 90 (45) mm length of upper (lower) edge, 45 mm height (B–D, F); 65 mm side length (E). The size of the orange pattern elements is drawn in proportion to the size of the dummy. The relative frequency of approaches to each dummy of a pair are indicated by the *height* of the *hatched bars* and the *numbers* at the side of each bar. The standard error of the mean given in the figures is calculated by assuming a binomial distribution of the choice behavior (see text). The number of approaches and the significance levels are given *below the histograms*

terflies prefer one of them because of its location in the greenhouse, rather than owing to its pattern. After 40 approaches, a different pair of dummies was tested. Since pattern discrimination behavior might differ between the sexes, in this study only the approaches of males were counted; they seem to approach the dummies more frequently than do females.

The choice frequency α of one of the dummies is given by the ratio of the number of approaches towards this dummy to the total number of approaches. The choice frequency of the alternative dummy, thus, is $1-\alpha$. $\alpha = 0.5$ implies that the butterflies do not discriminate between the two wing patterns, while $\alpha = 1$ or $\alpha = 0$ indicates perfect discrimination (with a preference for either one or the other pattern). The binary choice behavior of the lurcher follows a binomial distribution. This was confirmed by comparing the choice frequency expected on the basis of the binomial model for a group of either four or ten choices with the experimentally determined choice frequency (χ^2-test, $\alpha > 0.10$). Hence, for a choice frequency α measured on the basis of n responses, an estimate of the standard error of the mean (SEM) is given by $[\alpha(1-\alpha)/n]^{1/2}$. SEMs determined in this way are shown in Fig. 1. The difference between the measured choice frequency and the random-choice probability ($\alpha = 0.5$) was tested for significance, using the χ^2-test.

In a first set of experiments, it was tested whether the pattern on the wings matters in attracting the butterflies or whether any moving target is equally attractive to them. This was done by presenting a "standard" dummy which is characterized by two orange stripes parallel to its lateral edges, together with either a completely black or a completely orange dummy of the same size and shape (Fig. 1 B). The standard dummy was approached far more frequently than either the black or the orange dummy, showing that the pattern on the wings strongly affects its attractivity.

The specificity of the pattern discrimination abilities of the Australian lurcher was analyzed by presenting the standard dummy together with a dummy that differed in certain pattern parameters. Figure 1 C illustrates that the width of the orange stripes has a strong effect on the spontaneous preference for a dummy. The width of the stripes was either increased to twice the width of the stripes of the standard dummy or alternatively decreased to half their width. In both cases, the dummies were much less attractive than the standard dummy (upper two panels in Fig. 1 C). Hence, there is an optimal stripe width. The dummies with the narrow and broad stripes are approached with approximately the same frequency (bottom panel in Fig. 1 C).

In addition to the broad orange stripes across both the fore- and the hindwing, Australian lurchers possess a small dot close to the apical edge of each forewing (Fig. 1 A). To test the role that this dot plays in recognizing conspecifics, butterflies were given a choice between the standard dummy and one that had, in addition to the stripes, two small orange dots in the appropriate locations (Fig. 1 D). Although the dots are relatively small in size, they increase the attractivity of the dummy significantly. Since in the lurcher the sexes differ with respect to the color of the dot on each forewing, we are presently investigating whether this characteristic may play a role in sexual discrimination.

In preliminary experiments it was observed that lurchers not only approach dummies with stripes but are also attracted by dummies with more compact patterns, such as two large dots each centered in one half of the dummy. This characteristic could be exploited to test whether pattern preferences are invariant with respect to the orientation of the pattern as a whole because the dots, on their own, do not exhibit an inherent orientation. Since only the pattern on the wing, rather than the overall shape of the dummy, was to be varied, a quadratic shape was chosen for the dummy (Fig. 1 E). The choice frequencies obtained for the two perpendicular pattern orientations show that the dummy with the dots aligned along the horizontal axis is more attractive than the one with the dots aligned along the vertical axis. Hence the orientation of the pattern as a whole matters. Butterflies seem to prefer a bilaterally symmetrical pattern with a vertical plane of symmetry (which would agree with the natural wing pattern) over one with a horizontal plane of symmetry (which is unlike the natural pattern).

All of these examples show that the wing pattern greatly affects the choice frequency in favor of a particular dummy (see also [5]). In contrast, even considerable changes in the form of the black cardboard body of the dummy on which the orange pattern elements were offered did not influence the attractivity of a given pattern. Figure 1 F shows one example in which the standard dummy was tested against a dummy that was presented upside-down, with the orientation of stripes, however, being the same in both. Both dummies are approached with the same frequency. Hence, the pattern on the wings, rather then the wing form, appears to be the relevant visual cue for pattern discrimination.

Although it is commonly held that pattern information is not particularly important in the context of butterfly communication [3], these initial behavioral experiments on visual pattern discrimination of the Australian lurcher, *Yoma sabina*, clearly reveal that this butterfly uses visual pattern cues in selecting a target such as another butterfly. Owing to the limited spatial resolution of insect eyes and the relatively small size of the animals, visual pattern cues can only be used in recognizing conspecifics at distances of up to approximately 1 to 2 m. Of course, the present findings are not meant to imply that chemical signals such as pheromones are not significant in the recognition of conspecifics (for review see [6]). The functional role of the visual pattern-dependent interactions is not clear so far, as males seem to approach females as well as other males in a similar way, at least in our greenhouse. It needs to be worked out whether intersexual approaches differ from intrasexual ones. Still, it appears to be likely that the mechanism underlying pattern discrimination in the lurcher plays a role in intraspecific communication. This conclusion is based on the finding that, in the pairs of dummies tested in the present study, the dummy that resembles a lurcher more than the alternative dummy does is preferred (Fig. 1 B–D), even when the resemblance is only very rough (Fig. 1 E). Thus, the results shown here suggest that lurchers seem to use whatever parameter is available to them, if only it resembles the natural pattern in one way or another, whether the resemblance involves local details (Fig. 1 D) or global ones (Fig. 1 E). Spontaneous shape preferences of honeybees have led to similar conclusions [7]. It should be noted that preliminary experiments on the lurcher indicate that specific dummies (e.g., those with two compact orange dots, see Fig. 1 E) may be as attractive or even more attractive than what appears to human observers to be most lurcher-like. We are presently investigating the role of further shape parameters by systematically varying them, to determine which individual features, or combinations of such, are the most effective in the task of pattern discrimination. In addition, we plan to employ electrophysiology in order to find the neuronal mechanisms underlying the observed choice behavior.

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