

VISUAL STIMULI RELEASING ATTACK OF A TERRITORIAL MALE IN *SYMPETRUM* (ANISOPTERA: LIBELLULIDAE)

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Visually released responses to a rival male were studied in territorial males of *S. sanguineum*, *S. vulgatum*, *S. flaveolum* and *S. pedemontanum* using a fishing-rod to present synthetic models. Film discs with the dark body centre and the concentric wing spot (if necessary) turned out to be most effective. Position and presence of the abdomen made no difference. The species devoid of wing patterns (*S. sanguineum*, *S. vulgatum*, *S. danae*) are unable to recognize each other by appearance. Probably, they utilize other means of interspecific isolation. The species decorated with wing spots certainly distinguish conspecific males by the specific feature of pattern: an orange pericentral fleck in *S. flaveolum*, a subapical band in *S. pedemontanum*. The wing pattern shows stronger contrast in UV than in long wave rays. *S. sanguineum* showed moderate aggression against patterned models, but was less selective to various models than the two patterned species. The properties of the neural perceptor detecting the configurational visual stimulus are discussed. Distant recognition of the conspecific mate by its pattern is more reliable if the latter is restricted to basal or apical flecks and bands, while the wing middle remains clear. Most odonate species with wing decoration support this rule.

INTRODUCTION

Dragonflies rely mainly on their visual sense in their interaction with the environment. Visual stimuli are significantly important in the set of isolating factors, from ecological to mechanical ones. The role of the visible pattern in male-female recognition has been investigated by many authors. There are, however, fewer experiments and field observations concerning the problem of the territorial male recognizing its rival. (Tab. 1). The distant recognition of a conspecific rival is energetically advantageous, for the male avoids useless fights with strange species. Some observers stated that territorial odonate males lack

Table I
Visible features of a conspecific male for dragonflies

Species	Method	Meaningful features						References
		Body size	Body colour	Wing movements	Wing coloration	Wing display	Abdomen display	
<i>Hetaerina americana</i> , <i>H. titia</i> <i>Calopteryx</i>	field observation painting of live insects					+		JOHNSON, 1961 HEYMER, 1973
<i>Libellula pulchella</i> <i>L. luctuosa</i> , <i>Erythemis simplicicollis</i>	field observation painted insects on a fishing rod	+		+	+			PEZALLA, 1979 ANDREW, 1966
<i>Leucorrhinia dubia</i> , <i>L. rubicunda</i> <i>L. caudalis</i>	live insects on a fishing rod field observation				+		+	PAJUNEN, 1962, 1964 PAJUNEN, 1964
<i>Orithetrum albistylum</i> <i>Perithemis tenera</i>	field observation painting of live insects		+					ITO, 1960 JACOBS, 1955
<i>Plathemis lydia</i>	painting of live insects, field observations		+				+	JACOBS 1955; CAMPANELLA & WOLF, 1974
<i>Nesciothemis nigeriensis</i> <i>Pachydiplax longipennis</i>	painted insects on a fishing rod field observation, spectrophotometry	+	+					PARR & PARR, 1974 JOHNSON 1962; ROBEY, 1975
<i>Cordulia aenea</i>	dead insects on a rod				flight direction		abdomen shape	UBUKATA, 1983

proper discrimination of specific features and perform aggressive reactions against dragonflies of other species, genera, and families: *Lestes viridis* (DREYER, 1978), *Tanypteryx hageni* (CLEMENT & MEYER, 1980), *Cordulia aenea* (UBUKATA, 1975), *Leucorrhinia caudalis* (PAJUNEN, 1964), *Libellula quadrimaculata* (ZAIKA, 1977), *Orithetrum cancellatum* (KRÜNER, 1977), *Micrathyrina atra* (MAY, 1980), *Pachydiplax longipennis* (ROBEY, 1975) etc.

Anisopterans of the genus *Sympetrum* seem to be a promising subject for studying visual releasers of male aggression. The site of observation was populated by 5 species of that genus, viz. *S. sanguineum* (Müll.), *S. vulgatum* (L.), *S. flavòolum* (L.), *S. danae* (Sulz.) and *S. pedemonianum* (Allioni). Their seasonal and spatial distributions overlap broadly. It was possible to find some places where males of 4-5 species establish their territories at the same time. *S. sanguineum* males share the habitat with males of each species.

METHODS

Field experiments were carried out in the vicinity of Kiev, from July to September 1981-1982, from 12.30 hrs until 16.30 hrs local time on sunny days.

Presenting the models of dragonflies by the fishing-rod technique (ST. QUENTIN, 1934), we scored 5054 responses to 72 different models. All models were made of synthetics such as resistors, coloured pieces of insulation, and transparent or stained acetate film.

The observer showed a certain model up to ten times, proceeding from one male to another, then changed it to another one. A specific model, standard for the given species, was included in each set of experiments to check the seasonal and weather variation in male activity. The difference in

responses to different models was analyzed using the χ^2 test. Models were presented within 0.5-2.0 m of a resident male. Responses of males fall into four types, classified as:

(1) Attack: a model was approached to within 5 cm, up to a clash; aerial manoeuvres of the model were repeated.

(2) Survey: a straight exploratory flight to the model up to a distance of more than 10-15 cm, then return. Territorial males approached models from below. Attempts to attain an in-tandem position were witnessed only twice.

(3) Escape: flight from the territory without any attempt to return. Escape could have been elicited also by the movements of the observer.

(4) Indifference: no take off.

Transmission spectra of dragonfly wings were recorded by the Specord-Zeiss spectrophotometer. Wing transmission in UV was visualized by placing wings on a fluorescent yellow plate under black light.

Eye segments were excised by hand from Bouin fixed preparations. Directions of surfaces and axial structures were measured with a goniometer under a dissection microscope.

RESULTS

SPATIAL AND TEMPORAL DISTRIBUTION OF SPECIES

According to several years' observations, *Sympetrum* imagines emerge in the following order: *S. flaveolum*, *S. sanguineum*, *S. pedemontanum*, *S. danae*, and *S. vulgatum*. *S. flaveolum* territorial males are the first to undergo their maturation (at the end of July), and almost without delay they are followed by *S. sanguineum* and *S. pedemontanum*. The males of *S. vulgatum* start mating at the end of August. All five species are active in September and survive till the first frosts in October, though the relative abundance of *S. flaveolum* and *S. pedemontanum* apparently decreases at the end of the flying season.

S. sanguineum occupies territories at the side of water, in bogs, in wet and in dry riverside meadows, the first three habitats being shared with *S. flaveolum*. The males of *S. flaveolum* are more aggressive. They reside presuma-

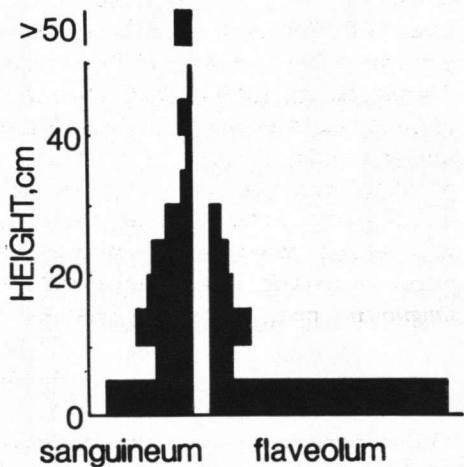


Fig. 1. Height of perching above the ground (cm) in territorial males of *S. sanguineum* and *S. flaveolum*. (Temperature 21-22°: — 170 and 62 records; — the areas of the histograms are normalized to unity).

bly on the surface or just above the ground. *S. sanguineum* males tend to perch somewhat higher on the grass or on shrubs (Fig. 1). When the weather is cool they descend to the surface. The males of *S. pedemontanum* are rather scarce. They gain territories on the sides of clear slow runnels or on the vegetation above the water, where *S. sanguineum* males reside as well. The males of *S. vulgatum* occupy territories in the paths amidst dry bottom meadows; other *Sympetrum* species rarely accompany them. Unfortunately we failed to find the sites where territorial males of *S. danae* swarm, though the mass emergence, hunting, and oviposition of this species were easily observable.

INTERSPECIFIC DIFFERENCES OF MALES

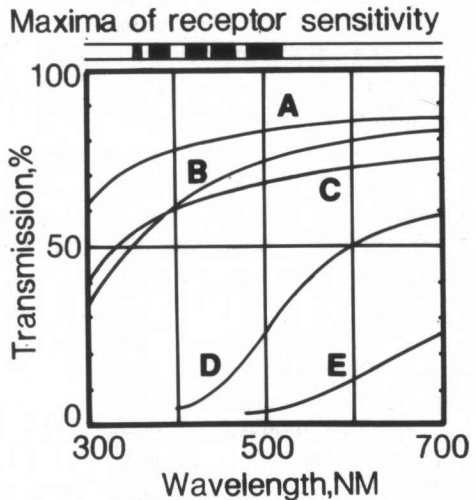
The features of five *Sympetrum* species are listed in Table II. An experienced observer can identify the species of *Sympetrum* either settled or even on the wing, practically without error.

Table II
Characteristics of *Sympetrum* males observable in the field

Species	Body length (mm)	Wing span (mm)	Body colour	Wing plate colour	Wing pattern
<i>sanguineum</i>	33.6 ± 1.2	55.0 ± 2.6	blood-red	slightly dusky	negligible
<i>vulgatum</i>	39.3 ± 2.0	58.8 ± 1.4	cherry-red	brownish	absent
<i>flaveolum</i>	33.6 ± 0.7	57.3 ± 2.4	orange-red	clear	basal yellow spot on hind wing (27% of wing area)
<i>danae</i>	31.7 ± 0.4	49.4 ± 1.3	black	clear	absent
<i>pedemontanum</i>	31.8 ± 0.6	53.7 ± 0.7	coral-red	clear	subapical brown band (12% of wing area)

The histogram above Figure 2 illustrates the short-wave shift of colour vision in odonates relative to man. Thus one may expect that wings of dragonflies look different in UV rays and in visible rays. The transmission spectra of wing plates are shown in Figure 2, while Figure 3 illus-

Fig. 2. Transmission spectra of male *Sympetrum* wings: (A) *S. danae*; — (B) *S. vulgatum*; — (C) *S. flaveolum*, transparent part; — (D) *S. flaveolum*, orange mark; — (E) *S. pedemontanum*, subapical band. — The bars above the graph show the spectral sensitivity maxima of dorsal eye receptors in odonates, cited by LAVOIE-DORNIK et al. (1981).



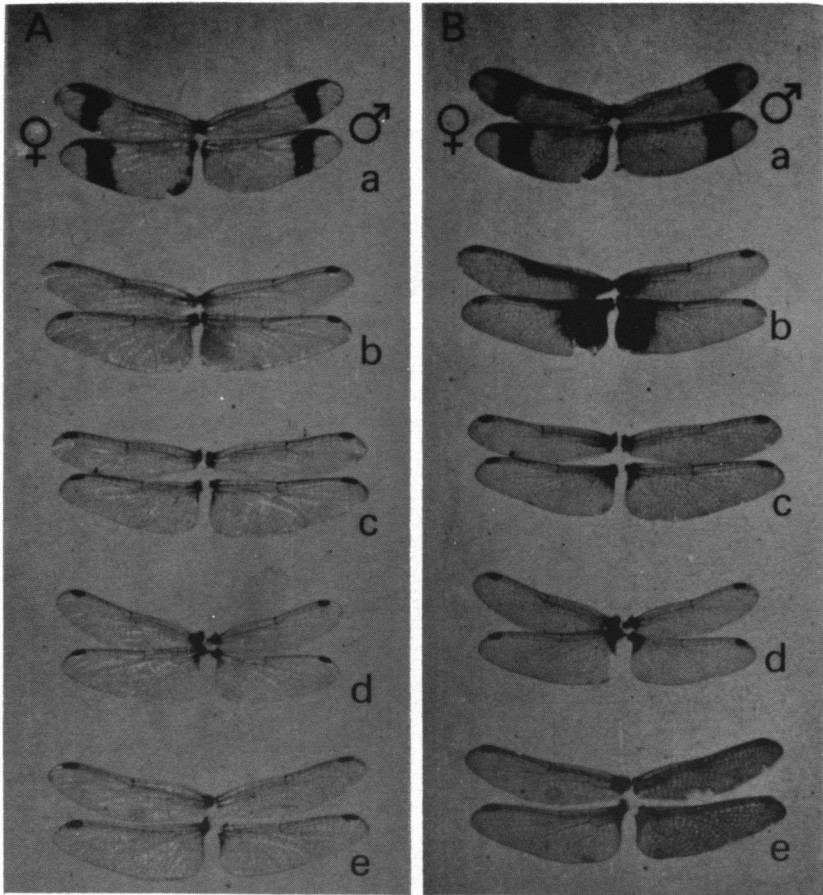


Fig. 3. *Sympetrum* wings against the yellow fluorescent plate: (A): in yellow light; (B) in UV light.

trates wing appearance in UV and long wave rays.

The wing decoration of *S. flaveolum* and *S. pedemontanum* looks much more contrasting for a dragonfly than for a human observer. Wings of *S. vulgatum* and *S. sanguineum* look dark compared with the transparent wings of *S. danae*.

BODY COLOUR

Dragonfly models were prepared from insulation of different colours. They mimicked the body shape of *S. sanguineum*: body length 34 mm, "thorax" size 12x6 mm, wing surface 10x40 mm. Responses of *S. flaveolum* and *S. sanguineum* males to these models are shown in Figure 4. The males approaching a model

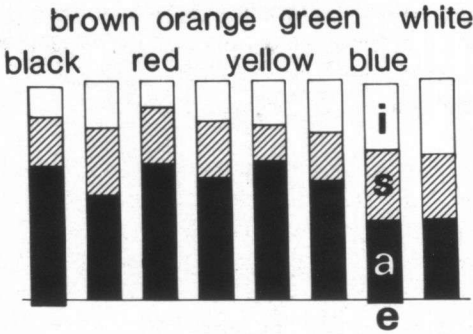


Fig. 4. Response frequencies of *S. sanguineum* and *S. flaveolum* males to colour models with transparent wings; 400 records. (a: attack; — e: escape [below the base line]; — i: indifference; — s: survey).

from below and viewing its silhouette against the sky cannot distinguish its colour properly. The significant preference of yellow and red models was observed only in comparison with white and blue ones. Thus, it seems improbable that *S. sanguineum* can distinguish the red conspecific rival from the black male of *S. danae* by body colour.

In the following experiments only red-bodied models were presented.

BODY SHAPE

Responses of *S. sanguineum* and *S. flaveolum* to models with transparent wings did not differ significantly and were pooled together. Most of the models were prepared from red resistors (12x6 mm), pieces of red insulation, and film plates (10x40 mm) or film discs (diameter 40 mm).

The results are shown in Figure 5, where the percentages of attack and survey are plotted along the two axes. The frequency scale underwent the transformation $\varphi = 2 \arcsin \sqrt{p}$, which provided the uniform scale of error over the whole range of frequency. The graph is

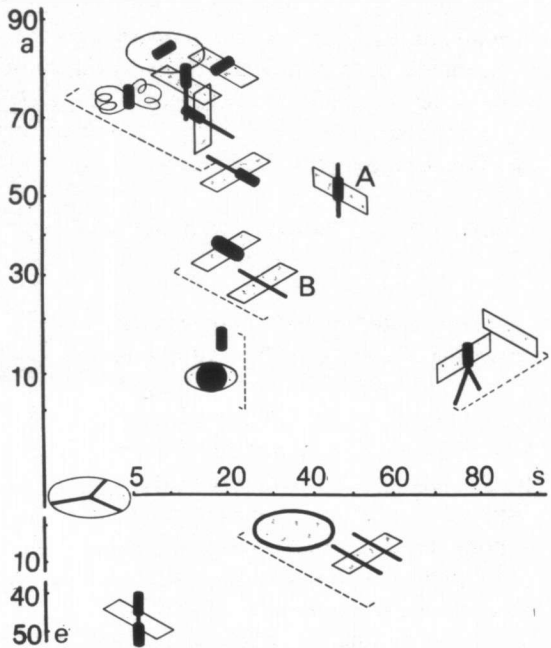


Fig. 5. Responses of *S. sanguineum* and *S. flaveolum* males to models of different shape. Models are drawn in isometry. Clusters of models eliciting statistically similar responses are enclosed by dashed lines. 2080 records. (a: attack; — e: escape; s: survey; for labels A, B cf. text).

limited by a diagonal connecting 100% points of attack and survey, both being positive behavioral alternatives. Ignored models occupy the part of the graph near both zeros. Attractive models yielded the escape rarely (< 2%). The prominent escape reaction is plotted along the negative ordinate values. Deterrent models were not attacked.

The most important positive features of the rival model were the presence of wings and a dark centre of certain size (30-70 mm²). Even the empty wing without any body was attractive. From the optical viewpoint, a wing hinders or reflects about 10% of incident rays. The film wing might be successfully replaced by several loops of thin wire. Horizontally suspended models were not stabilized and rotated on a line. They were less attractive for dragonflies than vertically suspended models. Rotation of a model in the latter position did not affect the stability of the image.

Model positions head up and head down were equivalent. Dragonflies responded similarly to "thorax" lacking models (labelled "B" in Fig. 5), aerially stabilized in various positions.

The annular model and models with multiple parts (bodies or tails) failed to elicit an attack but provoked an escape. Responses to the model with a "thorax" in the middle of the tail (labelled "A" in Fig. 5) differed between *S. sanguineum* (89% surveys) and the more aggressive *S. flaveolum* (94% attacks).

The most attractive bait, with a releasing rate of 90-95%, was a film disc with a compact dark centre.

BODY SIZE AND WING COLORATION IN *S. VULGATUM*

We presented models progressively increasing in size from 27 to 50 mm to males of *S. vulgatum* and *S. sanguineum* (Fig. 6), model "B" imitating the male of *S. vulgatum*, and model "C" that of *S. sanguineum*. We observed no distinct correlation between size and response type. The maxi model "A" was discovered and intercepted within a distance of 3-4 m, models "B" and "C" within 2-3 m, and the mini model "D" within 1-2 m.

The wings of mature *S. vulgatum* males are more obscure than those of *S. sanguineum*. Males of *S. vulgatum* distinguished the model with film wings

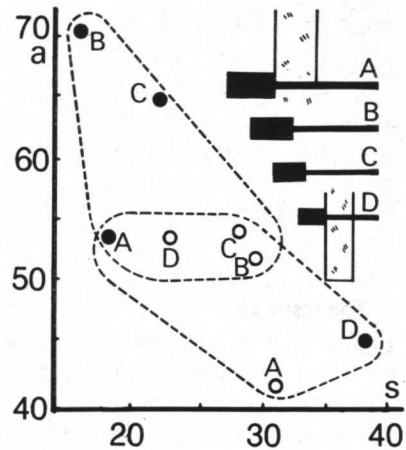


Fig. 6. Responses to models of different size (A-D) in males of *S. sanguineum* (open circles) and *S. vulgatum* (solid circles). Clusters of models eliciting statistically similar responses are enclosed by dashed lines. 605 records. (a: attack; — s: survey).

stained with picric acid, which was opaque for UV (17% attacks), from the model with transparent wings (62% attacks). But the clear wing was indistinguishable from the dark one, prepared from the film almost cleaned of picric stain (53% attacks, total 151 records).

It appears unlikely that *S. sanguineum* and *S. vulgatum* can discriminate each other by size or wing coloration.

WING PATTERN IN *S. FLAVEOLUM*

Models with an orange basal fleck (even blue or coal-black) in the empty wing sufficed to for the males of *S. flaveolum*. An empty wing with a central orange fleck was also intercepted (Fig. 7). The presence of the central orange fleck added some attraction to annular and double-bodied models. Models with a displaced orange fleck produced no attack.

The presence of a coloured fleck (even blue or coal-black) in the empty wing sufficed to attract the male of *S. flaveolum* (Tab. III). It is worth noting that the fleck stained with an orange-tip pen elicited furious attacks and differed in this respect from the picric-stained ultra-black fleck, the latter being usually surveyed but rarely attacked.

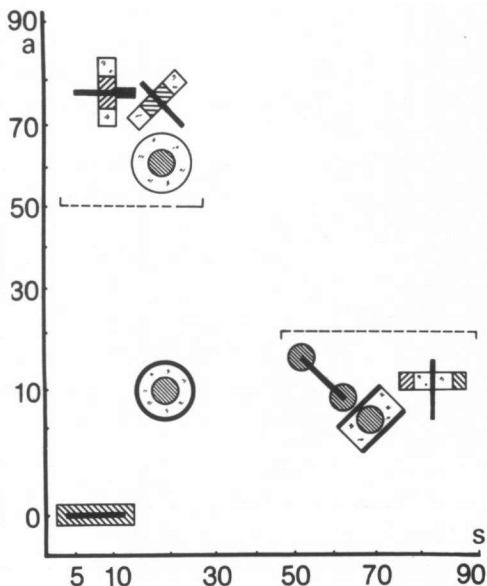


Fig. 7. Responses of *S. flaveolum* male to models with various positions of an orange mark (shaded areas). Clusters of models eliciting statistically similar responses are enclosed by dashed lines. 419 records. (a: attack; — s: survey).

Table III
Responses of *Sympetrum* males to the wing plate with a colour spot

Spot colour	N	<i>sanguineum</i>		N	<i>flaveolum</i>	
		Attacks (%)	Surveys (%)		Attacks (%)	Surveys (%)
Clear	29	14	86	24	0	4
Orange	46	13	59*	64	91	5
Picric yellow	49	4	47*	53	15	55
Blue	—	—	—	40	65	30*
Black	39	5	44*	79	54	48*

* responses do not differ significantly at the 5% level.

The presence of the basal orange fleck gives *S. flaveolum* the possibility to discriminate models resembling its own species from the models of *S. sanguineum* (Fig. 8). The model with a large orange fleck covering half of the wing was supraoptimal. The χ^2 test for uniformity revealed that responses of *S. flaveolum* to different models were more heterogeneous than those of *S. sanguineum* ($\chi^2 = 121.6$ and 18.8 respectively; 6 d.f.; escape and indifference pooled together).

WING PATTERN IN *S. PEDEMONTANUM*

The models attracting *S. pedemontanum* are illustrated in Figure 9. Models with apical wing bands were almost 100% attractive, though attacks were directed mainly at models with a "thorax". The model with apical bands and supranormal wing span (70 mm), which is omitted in Figure 9, elicited take-off at every demonstration (95% attacks).

The band coloration, viz. orange, brown, coal-black, picric-yellow (= ultra-black), or purple (UV transmitting saffranin stain), had no significance. Models without wing decoration or with a basal fleck were regarded with indifference.

The presence of apical bands allows *S. pedemontanum* to discriminate with certainty the models resembling its own species from the models of *S. sanguineum* (Fig. 10). The "turbo" model with a wing disc, black marginal sectorial pattern, and a dark compact centre was supraoptimal. It was furiously intercepted by males; the rustle was heard from the clash of the pursuer with the bait.

Responses of *S. pedemontanum* to various models exhibited pronounced selectivity as compared with *S. sanguineum* ($\chi^2 = 200.3$ and 32.5 respectively).

EYE RESOLUTION

In the frontal part of an eye the facet rows are directed along the equator (z

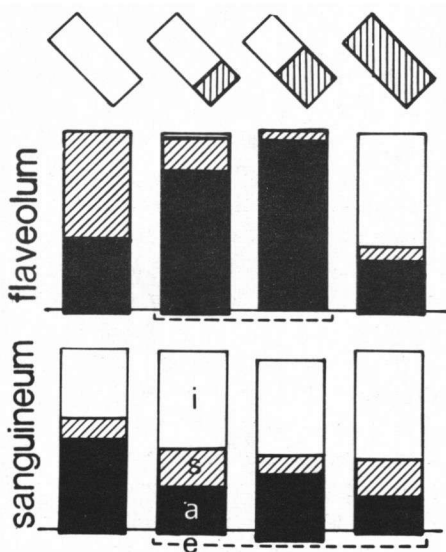


Fig. 8. Discrimination of the species-specific model by its wing pattern in *S. sanguineum* and *S. flaveolum*. Wing pictures are shown above the graph (shaded areas indicate orange marks). Models eliciting statistically similar responses are enclosed by dashed lines. 468 records. (a: attack; — e: escape (below the base line); — i: indifference; — s: survey).

row), from the medio-superior to the latero-inferior corner (x row), and from the latero-superior to the medio-inferior corner (y row). Proceeding to the dorsal eye segment, the rows rotate about 90° - 120° (clockwise in the right eye). Divergence of ommatidia is unequal in different rows and varies inside the row (Fig. 11).

The divergence angle $\Delta \varphi$ among the optical axes of adjacent ommatidia comprise on average 1.2° , 0.6° , and 1.1° in the x , y and z rows respectively, being slightly less than the anatomical divergence due to the inclined position of the ommatidia to the cornea. In general $\Delta \varphi$ values in the dorsal part of an eye of *Sympetrum* are about 0.9° - 1.0° .

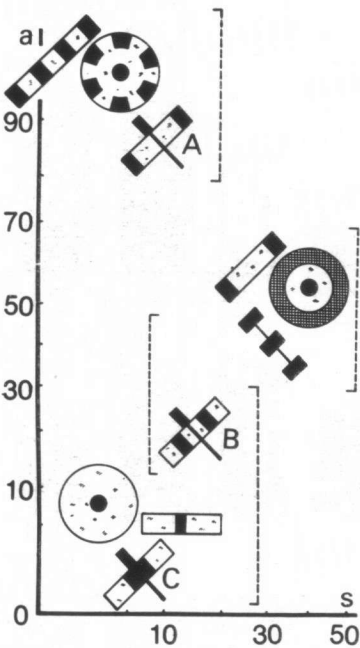


Fig. 9. Response of *S. pedemontanum* males to models of various shape. Clusters of models eliciting statistically similar responses are enclosed by dashed lines. 460 records. (a: attack; — s: survey; for labels A, B, C, cf. text).

S. sanguineum occupies light stones (HEYMER, 1969); *Leucorrhinia caudalis* perches on floating leaves, *L. dubia* rests on various substrates (PAJUNEN, 1964).

The species without wing spots (*S. sanguineum*, *S. vulgatum*, and *S. danae*) are obviously unable to discriminate rivals of their own and strange species by their appearance. That is why habitat selection provides certain spatial isolation in

DISCUSSION

VISUAL STIMULI IN INTERSPECIFIC ISOLATION

Sympetrum species, which have a conspicuous wing coloration, viz. *S. pedemontanum* and *S. flaveolum*, distinguish reliably the conspecific insect among other dragonflies. This ability is especially important for *S. pedemontanum*, scarce at the study site, which must find a conspecific mate within the outnumbering population of other dragonfly species.

S. sanguineum, devoid of wing decoration, has a less limited pattern selectivity. The presence of features alien to the insect decreases model attractiveness, but does not cancel it. Vision also contributes to the partition of settling sites in the same locality between *S. sanguineum* and *S. flaveolum*, which may serve as an additional isolating cue.

Partition of residence sites among congeneric males has been reported for other libellulids: *Orthemum coerulescens* perches on branches, whereas *O. brun-*

territorial males, despite oviposition in the same bog.

INNATE IMAGE OF A RIVAL

It seems strange that, for dragonflies with their excellent vision, the most efficient stimulus releasing the attack has been reduced either to the simple concentric configuration composed of a compact body, a wing disc, and a pericentral or marginal pattern (Fig. 12), or to its linear version.

The doubling of body parts switches an attractive model to a deterring one, but it is hard to believe that the only reason for this alteration is the lateral inhibition reducing contrast of the neural image of a double model.

From a human viewpoint, the long abdomen is a sign distinguishing odonates among other insects. We expected that males would recognize the bar oriented along the direction of motion, a sort of "worm" versus "antiworm" configuration detectable by amphibians (EWERT & v. WIE-TERSHEIM, 1974). Contrary to expectation, the tests with models revealed that position and even absence of abdomen had no effect on the attacking *Sympetrum* male. Indeed, a male attacking a rival during a chase or during head-to-head spiralling, will see it without a prominent abdomen.

It is difficult to decide whether this simplification of the releaser represents a primary or secondary state. All Zygoptera use abdominal warning to drive away their approaching mates. Abdominal lifting symbolizes the male for a *Calopteryx* female (HEYMER, 1973) and for a male of *Plathemis lydia* (JACOBS, 1955, CAMPANELLA & WOLF, 1974). Nevertheless, such simple design of the innate releaser encourages us to seek for its simple perceiving copy in the visual centres.

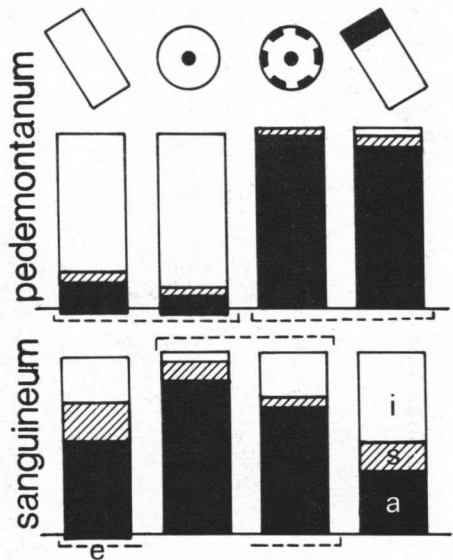


Fig. 10. Discrimination of the species-specific model by its wing pattern in *S. sanguineum* and *S. pedemontanum*. Wing pictures are shown above the graph. Models eliciting statistically similar responses are enclosed by dashed lines. 496 records. (a: attack; — e: escape [below the base line]; — i: indifference; — s: survey).

PERCEPTOR: A SYSTEM OF COAXIAL SPATIAL FILTERS?

At large distances, where angular subtension of a target is less than eye resolution, all visible features of the target focus to a point in which the shading against the sky, light flux modulation exerted by wing fluttering, spectral filtration through the wing pattern, etc. are mixed. At distances inside the critical range, the spatial order of certain parts of a target becomes noticeable.

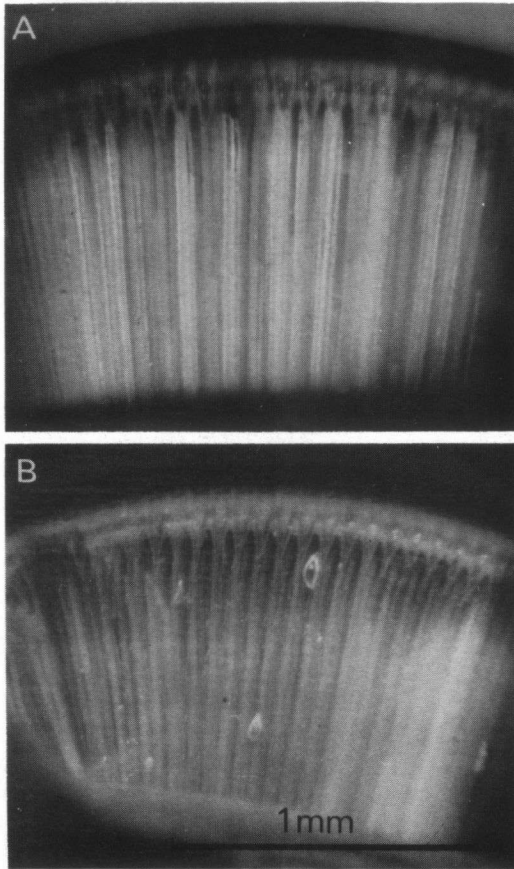


Fig. 11. Eye segments from the dorsal part of *Sympetrum* eye, excised along the y row of ommatidia (A) and along the z row (B).

The concept of perceptor as of a configurational field of neural circuits, intended to detect some configurational visual stimulus, was proposed by JANDER & VOLK-HEINRICHS (1970). The perceptor for stimuli depicted in Figure 12 must join features of different quality.

We infer this since even incomplete models preserve some moderate attractiveness, e.g. a wingless body, an empty wing, a coloured fleck. Probably those features are detectable by independent neural layers in a retinotopic projection. Integration into a perfect image accords with the principle of the sum of stimuli and obeys the following rules: (1) certain features are situated

in a definite order; and — (2) recognition of optimal order is invariant upon distance of the standard target.

Distance alters the angular subtension of a target as well as the area covered by detail of the image on the retina. Thus the intensity of retinal signals alters also.

Under such circumstances some relationship is expected between intensity of local retinal excitation and acceptable distance between excited loci in the receptive field.

The pattern of *S. pedemontanum* males might serve as a challenge object to test the perceptor model detecting a dark centre, surrounded by an obscure or flickering annulus. Let us suggest that around the image of the dark centre in the retinal projection an annular zone emerges which perceives with particular sensitivity the independent image of wing bands.

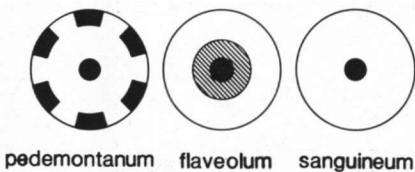


Fig. 12. Concentric patterns releasing the attack in a territorial *Sympetrum* male, as indicated.

There exists a well known model producing the annular zone of altered sensitivity. It consists of a pair of concentric linear filters. The low-pass filters have gaussian or exponential characteristics with unequal parameters. The difference between output signals runs through its extreme at a certain distance from the centre. The radius of the extreme annulus depends on the parameters and gains of the

filters. Since the filter parameters are hardware in the neural network, the radius of the annulus may be controlled only by a change of response amplitudes. If the filter output signals are maintained at a constant proportion under various input intensities, then the position of their maximal difference would also be stable. Therefore the outputs of the exciting and inhibiting filters have to change quite definitely with respect to the image intensity in order to adjust the width of the annular zone to the change in intensity. The intensity-response functions of neurones in the complicated spatial filter must be mutually nonlinear.

Obviously, static linear filtering is not the only possible explanation for detecting spatial proportions.

"FORBIDDEN" WING PATTERN

In comparison to a human observer a dragonfly sights another dragonfly not only in shifted hue but with fewer details (Fig.13). Angular sensitivity of ommatidia and the effect of lateral inhibition were neglected in this figure because they have no significance for the following considerations. Evidently the three elements of a concentric stimulus, namely the body centre, the transparent part of the wing and the coloured part could be resolved if the image was projected onto an area at least 5 facets in diameter. The critical distance at which the body and the apical band of *S. pedemontanum* are parted by the subtension of $2 \Delta \varphi$ is only 0.5 m. At a distance of 1-2 m the bands are seen like something flickering, apposed to the body centre.

For the purpose of distant recognition of conspecific insects by their wing decoration it would have been advantageous to place the pattern elements of the wing as close to or as far from the body as possible. The middle elements of the pattern could be resolved from the basal and apical ones only under close inspection. Is there a dragonfly with a pattern intermediate between the pattern of *S. pedemontanum* (Fig. 9 - A) and of *S. flaveolum* (Fig. 9 - C)? Such a hypothetical insect is depicted in Figure 9 - B.

In an effort to verify this assumption we checked all species in the collection of Odonata in the Museum of the Zoological Institute (USSR Acad. Sci., Leningrad). 190 species and subspecies possessed apparent wing decoration. In the following text they are called by the names with which they were labelled in the collection.

For further processing of the data any colour of the pattern, be it black, brown, red, yellow, white, metallic-blue, or -green, was considered as equivalent contrast against a transparent wing plate. Some species were polychromatic; one colour covered the basal part of the wing, another expanded over the periphery.

Typical examples of wing patterns are illustrated in Figure 14. The dendrogram of transitions between picture types does not reflect phylogenetic relations. The majority of odonates have distinct basal, apical, or subapical pattern details.

Eight species, or 4% (on the graph: from *Pseudoleon superbus* to *Thore batesi*) have a dark or a translucent white band drawn near the middle of the wing, but only in two cases does the band exactly halve the wing. Twenty species (10%) have a speckled pattern. Their representative pictures in the middle of the dendrogram are connected by dashed lines. This group includes species of *Rhyothemis*, *Palpopleura*, *Libellula*, etc. One species with longitudinal arrangement of pattern details (the male *Palpopleura lucia*) was not taken into consideration.

We know nothing about the meaning of certain pattern details for mutual recognition of odonates with the speckled or middle pattern. Is it important for those insects to see a wealth of detail, or are they satisfied with perception of overall diminution of light transmission? At any rate, the distinct recognition of a

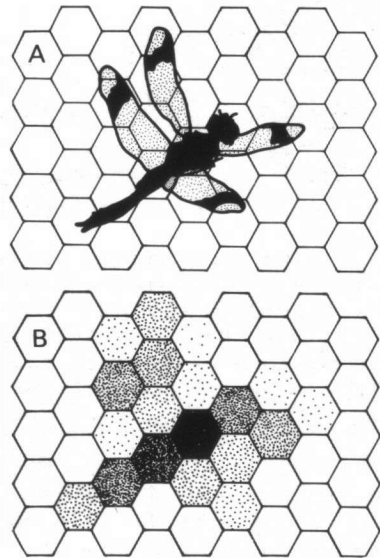


Fig. 13. *S. pedemontanum*: (A) a flying male against the facet lattice with $\Delta \varphi = 1^\circ$, viewed at a distance of 0.5 m; — (B) retinal image of the same object.

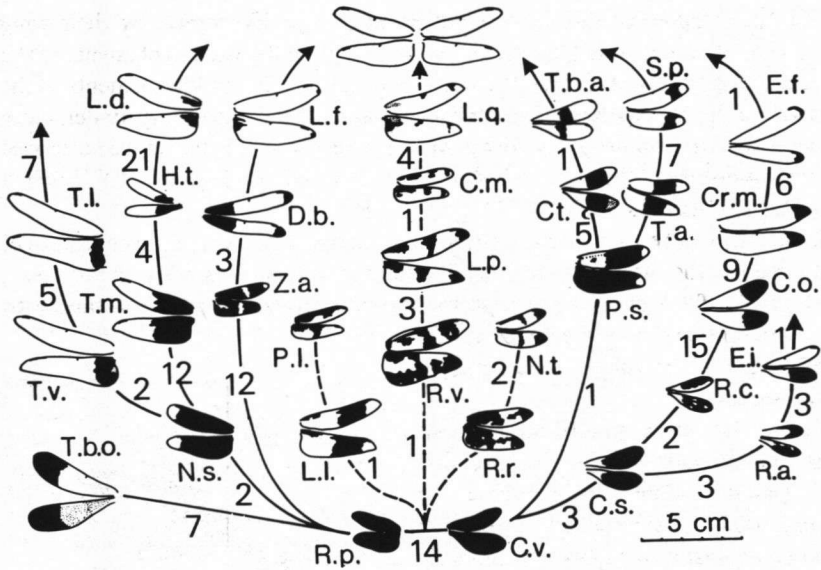


Fig. 14. The types of wing pattern in a representative collection of Odonata. The figures indicate the number of species transitional between the depicted forms. C.o.: *Calopteryx orientalis* Sel.; — C.s.: *C. splendens* (Harr.); — C.t.: *C. taurica* Sel.; — C.v.: *C. virgo* (L.); — C.m.: *Celithemis monomelaena* Wllsn; — Cr.m.: *Cratilla metallica* (Br.); — D.b.: *Dysphaea basitincta* Martin; — E.f.: *Epallage fatime* (Charp.); — E.i.: *Euphaea inaequipar* Sel.; — H.t.: *Hetaerina texana* Walsh; — L.d.: *Libellula depressa* L.; — L.f.: *L. fulva* Müll.; — L.l.: *Plathemis lydia* (Dru.); — L.p.: *L. pulchella* Dru.; — L.q.: *L. quadrimaculata* L.; — N.s.: *Neurothemis sophronia* (Dru.); — N.t.: *N. tullia* (Dru.); — P.l.: *Palpopleura lucia* Ris; — P.s.: *Pseudoleon superbus* (Hag.); — R.a.: *Rhinocypha angusta* Sel.; — R.c.: *R. cuneata* Sel.; — R.p.: *Rhyothemis plutonia* Sel.; — R.r.: *R. regia* (Br.); — R.v.: *R. variegata* (Joh.); — S.p.: *Sympetrum pedemontanum* (All.); — T.a.: *Trithemis attenuata* Kirby; — T.ba.: *Thore batesi*, Sel. ♀; — T.bo.: *T. boliviana* McL.; — T.l.: *Tramea limbata* (Desj.); — T.m.: *Thermodthemis madagascarensis* (Ramb.); — T.v.: *Tramea virginia* (Ramb.); — Z.a.: *Zenithoptera americana* Ris.

conspecific mate by wing pattern may be a problem for them, and indeed this group of Odonata is few in number — 12-15% of species with wing decoration.

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