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Mechanisms of plasticity in simple taxis behaviors in *Drosophila*

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1. Introduction

Like the proverbial moth drawn to the candle flame, the fruit fly Drosophila also stereotypically approaches light sources. This positive phototaxis is the archetypal example of hard-wired input-output behaviors. However, it has long been known that defects to the wings of the fly, either by mutation or by damage, reduce not only phototaxis but also geotaxis in walking Drosophila. If these behaviors are so hard-wired, how can manipulating an unrelated organ affect them? Using the classic countercurrent photo-/geotaxis essay developed by Seymour Benzer, we tested the hypothesis that instead of taxis being a simple matter of stimulus and response, there may be a central decision-making stage which is influenced by the wing manipulations.

2. Methods

Wings were manipulated under CO_2 anaesthesia in groups of 100 flies (50 were manipulated and 50 were left intact. The 100 flies were loaded into the first source tube of the Benzer counter-current apparatus, consisting of five target and six source tubes (see figure). Flies were tested for phototaxis with the apparatus oriented horizontally, with the target tubes towards a fluorescent tube. Flies were tested for geotaxis in the dark with the apparatus oriented vertically. Flies were tested for walking activity without sensory cues in the dark with the apparatus oriented horizontally. A phototaxis run lasted 15s, a geotaxuis run 30s and a walking activity run 60s. After 5 runs the experiment was ended and the flies were counted. From the number of flies in each tube, a performance index was calculated:

$$PI = [(0*F0)+(1*F1)+(2*F2)+(3*F3)+(4*F4)+(5*F5)]/\Sigma$$

The relative effect size of the wing manipulation was calculated from the PIs of manipulated and intact flies for each experiment:

$$S_{rel.} = (PI^{+} - PI^{-}) / PI^{+}$$

Fly strains used

vestigial	- Allele of the *vestigial* gene, "wingless"
Cnt-E	- Tetanus Toxin light chain (UAS effector gene), suppresses synaptic release
norp A	- have no receptor potetial, "blind"
Canton S	- Wild Type Canton S
Wtb	- Wild Type Berlin
mb247	- mushroom-body specific GAL4 driver line
FoxP	- Transposon in putative last exon of FoxP gene. Allele defective in operant learning
rut^{2080}	- *rutabaga*, hypomorphic allele of type I adenylate cyklase
w^{1118}	- Allele of the *white* gene, white eyes
w^{10}	- Allele of the *white* gene, white eyes
rsh^{161}	- *radish*, unknown gene involved in anaesthesia resistant memory
PKCi	- Inhibitory peptide suppressing Protain Kinase C activity (UAS effector egene).
hs-GAL4	- Heat-shock activated GAL4 driver line

3. Results

a) Recovery time

The effect of clipping flies' wings on their behavior is independent of recovery time after the manipulation. Relative effect size in both photo- and geotaxis varies little with recovery time.

b) Different wildtype strains

The effect of clipping flies' wings on their behavior is independent of the genetic background in different populations of wildtype laboratory strains.

c) Learning and memory

Manipulations of different processes involved in learning and memory have only little impact on the wing-clipping effect. There may be a quantitative contribution, but this remains to be confirmed

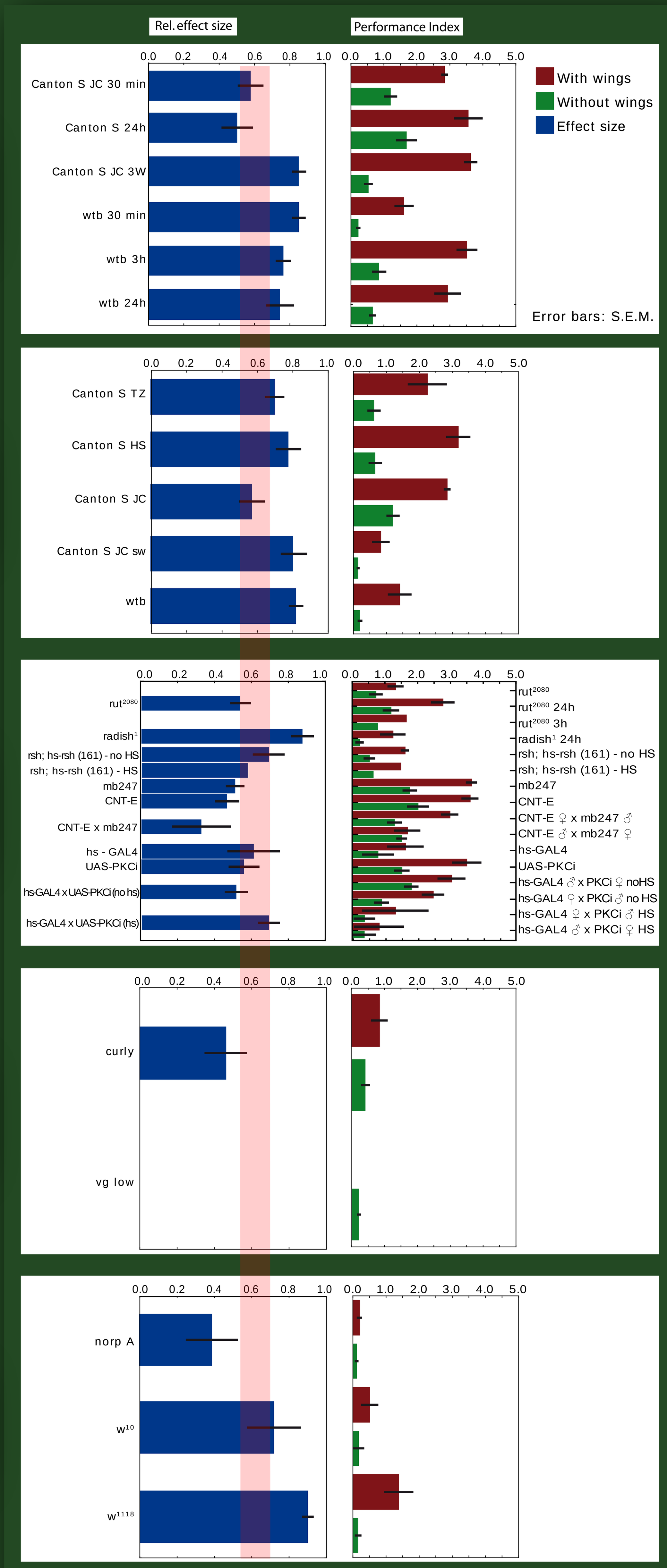
d) Flight ability

The wing-clipping effect is slightly reduced in phototaxis of flies who are already impaired in their flight ability by mutation. The effect is more pronounced ingeotaxis but still quantitative.

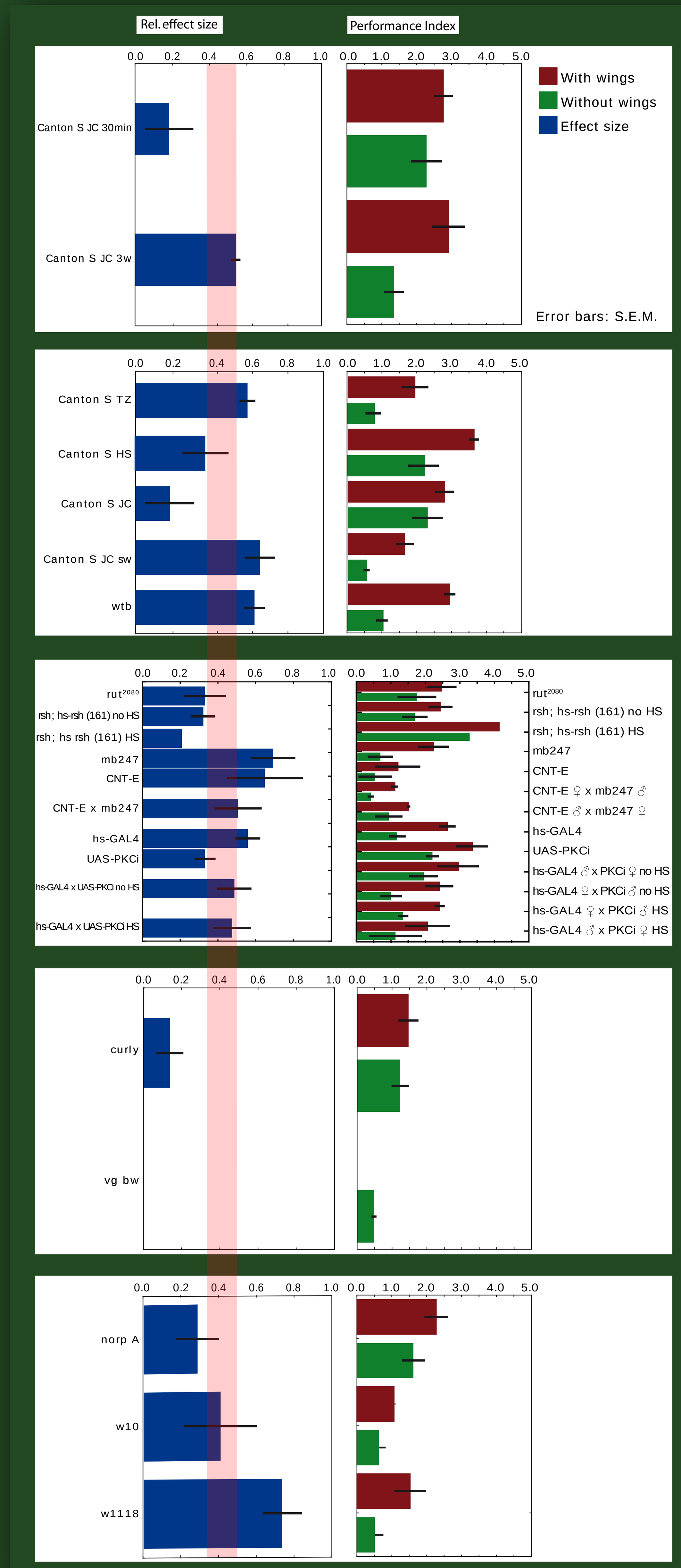
e) Vision

Different alleles imparing vision to different degrees have varying, quantitative effects either increasing or decreasing the reduction in photo- and geotaxis after wing clipping. Vision itself is probably not important for the effect.

Phototaxis



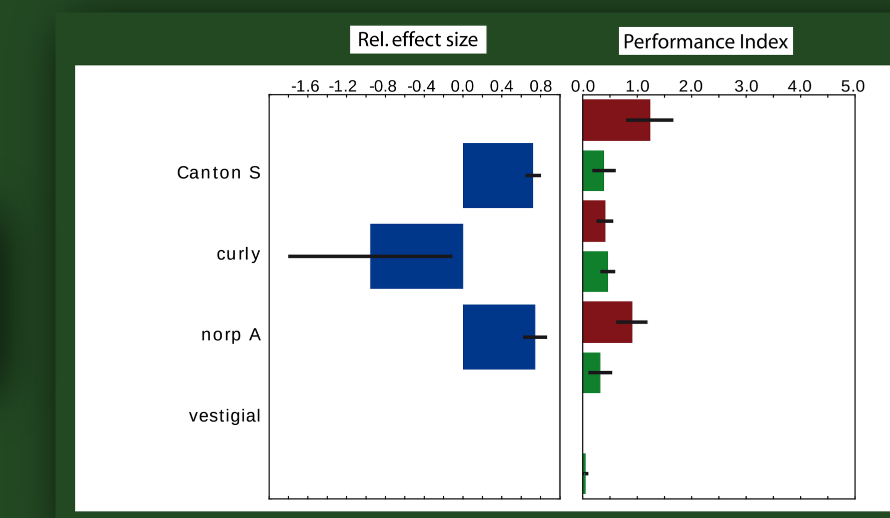
Geotaxis



Activity

f) General walking activity

If tested for general walking activity in the dark, wildtype and blind flies show the same reduction in activity after clipping their wings. However, this reduction is completely absent in *curly* flies which are unable to flie before the wing clipping.



4. Conclusions

Plasticity in simple behaviors not so simple

Simple taxis behaviors are considered to be hard-wired input-output systems: the sensory input triggers motor output via developmentally determined neuronal connections. Examples of such simple behaviors include the photo- and geotaxis tested here. However, even such simple behaviors show some degree of plasticity: walking flies whose wings have been cut show reduced taxis compared to intact walking flies. Indeed, they show less walking activity in general.

Robust plasticity

We have tested a large number of different wildtype and transgenic strains for their reduction in phtoto- and geotaxis as well as in general walking activity after clipping of their wings. In all but one case have the effects of these manipulations been only quantitative, if not marginal. We were only able to completely abolish the reduction after wing clipping in a single strain of flies in one single test case. General walking activity in flies who have not previously been able to fly (*curly* mutant flies) does not decrease further when the wings are clipped. Interestingly, this lack of reduction in walking activity appears to have only little or no effect on the reduction in photo- or geotaxis.

Two or more components contribute to plasticity

These results suggest that the plasticity observed even in 'simple' taxis behaviors is complex and consists of at least two components: an unspecific, general component and a component which is specific to the stimulus elciting the taxis behavior.

Experiments with flies impaired in various forms of learning and memory suggest that a small component may also be attributable to these processes. However, the effect was too small for any firm conclusions and requires more research.

Further research needed

We have only begun to scratch the surface of this form of plasticity. Dozens of candidate lines have been tested without clear-cut results. We have several additional types of experiments planned, including glueing the wings together, perforating the wings, manipulating major biogenic amine pathways and testing more strains with impaired flight ability.

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