Animal Behaviour 142 (2018) 207–220

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Now you see me, now you don't: dynamic flash coloration as an antipredator strategy in motion

Gopal Murali*

IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE), School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Thiruvananthapuram, India

ARTICLE INFO

Article history:
Received 1 March 2018
Initial acceptance 10 April 2018
Final acceptance 1 June 2018

MS. number: 18-00165R

Keywords:
animal coloration
antipredator adaption
butterfly
dorsoventral contrast
flash coloration
flash lag
position perception
shorebirds

Animals employ a diverse array of colorations to avoid being consumed by predators. While much research has focused on patterns that work when the animal remains stationary, studies examining the role of colour patterns that function when it moves to avoid predation remain scarce. Here, I propose and test the hypothesis that striking colorations that change dynamically through time, for example bright colours on the dorsal wing surface in combination with cryptic/contrasting ventral coloration (or vice versa) as seen in many insects and birds, serve to protect the moving animal from predation. This idea is analogous to a well-known visual illusion termed the flash lag effect which occurs because of the constraints in estimating the instantaneous position of a moving object due to the inherent neural processing delay. I performed a virtual predation experiment using a touch screen where human participants were asked to capture a moving stimulus that changed colour dynamically through time or remained constant. I found stimuli with dynamic colour change were caught less often and less accurately than a colour-static white or background-matching stimulus but were equally difficult to capture as a colour-static average grey under certain conditions. These results suggest that dynamic colour change is effective in lowering the probability of capture, but this benefit is not unique, as the colour-static average grey stimulus had a similar advantage. Overall, the study thus presents the first clear evidence that animals that change colours during movement could gain significant protection against predation, probably by misrepresenting the prey's location.

Camouflage is a protective strategy that works by preventing detection or recognition by predator or prey (Merilaita, Scott-Samuel, & Cuthill, 2017; Ruxton, Sherratt, & Speed, 2004; Stevens & Merilaita, 2009). This ubiquitous form of defence has been well studied for over a century and is frequently referred to as a textbook example of natural selection (Endler, 1980; Kettlewell, 1955). However, once the camouflaged animal moves, its boundaries are easily given away due to the 'motion contrast' between the surrounding background and the animal (Regan & Beverley, 1984; Zylinski, Osorio, & Shohet, 2009). Because of this, camouflage is suggested to work as long as the animal remains motionless (Hailman, 1977; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Ioannou & Krause, 2009). Given that animals need to move for reasons such as foraging and to search for mates, it is necessary to understand how predation can be reduced during motion and whether certain coloration could help animals achieve this.

One such defence strategy involving colours is the use of 'motion dazzle' patterns, which have been proposed to be used by many animals including zebras, fishes, snakes, frogs and lizards (Allen, Baddeley, Scott-Samuel, & Cuthill, 2013; Halperin, Carmel, & Hawlena, 2017; Hogan, Cuthill, & Scott-Samuel, 2016; Jackson, Ingram III, & Campbell, 1976; Murali & Kodandaramaiah, 2016; Rojas, Devillechabrolle, & Endler, 2014; Stevens, Searle, Seymour, Marshall, & Ruxton, 2011; Thayer, 1909). Motion dazzle patterns are typically high-contrast repetitive patterns, such as stripes, bands and zigzags, that influence the estimation of speed or direction of prey movement (Hughes, Jones, Joshi, & Tolhurst, 2017; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011) and thus lower the accuracy of prey capture (Stevens, Yule, & Ruxton, 2008). Another effect that mobile prey have been suggested to utilize is the 'flicker fusion effect' (Jackson et al., 1976), wherein high-contrast repetitive bands are perceived to blur at high speed, allowing the animal to blend in with the surroundings during movement (Umeton, Read, & Rowe, 2017). Both these ideas were initially proposed long ago

* Correspondence: G. Murali, IISER-TVM Centre for Research and Education in Ecology and Evolution (ICREEE), School of Biology, Indian Institute of Science Education and Research Thiruvananthapuram, Maruthamala PO, Vithura, Thiruvananthapuram 695 551, India.
E-mail address: gopal13@iisertvm.ac.in.

https://doi.org/10.1016/j.anbehav.2018.06.017
0003-3472/

(Pough, 1976; Thayer, 1909) but have gained significant attention recently (Hogan et al., 2016; Hughes et al., 2017; Murali & Kodandaramaiah, 2018; Umeton et al., 2017). Yet, given the vast diversity of colour patterns seen in animals, our understanding of defensive colorations that are effective in motion remains limited.

Many animals, for example insects and birds, have the dorsal and ventral sides of their wings coloured differently (Fig. 1c, d), causing a dynamic colour change during motion (Fig. 1b). Although the striking colour patterns of palatable insects (e.g. butterflies; Fig. 1d) have so far been thought to function as sexual signals (Fraser, 1871; Oliver & Monteiro, 2010), a few anecdotal reports suggest that such differential coloration that changes during flight ('dynamic flash coloration') might work as protection against predation. For instance, Young (1971) found certain species of *Morpho* butterflies (Fig. 1d) to have low predation rates and reasoned that dramatic change of colours with 'flashy bobbing' flight might make it less predictable for the predator to intercept during motion. Further, de L. Brooke (1998) suggested that flash marks in shorebirds (Fig. 1c), which typically alternate between a dark upper side and light underside during movement, might reduce predation by enhancing the confusion effect in predators. However, there is no direct experimental evidence linking dynamic colour change in motion with attack accuracy (but see Hall et al., 2016). Here, I briefly outline the challenge associated with estimating the instantaneous position of a moving object and demonstrate how dynamic flash coloration during prey movement can work as protection against predation.

Because of the relatively slow transduction of neural signals, the visual system requires tens to hundreds of milliseconds to process the images that strike the retina (Aho, Donner, Helenius, Larsen, & Reuter, 1993; Berry, Brivanlou, Jordan, & Meister, 1999). This inevitable delay has long been thought to lead to a 'lag' in the perception of sensory events (e.g. motion of the object: Nijhawan, 1994; Purushothaman, Patel, Bedell, & Ogmen, 1998). Such 'sensory lag' can be illustrated in the context of prey capture by a predator during motion (Fig. 1a). Consider a stationary predator (bird) that detects a moving prey (butterfly) at a position d_0. By the time the visual signal is being processed (Δt_v), the prey would have already moved to a new position d_1. In addition, prey would have further moved to position d_2 because of the delay (Δt_m) incurred by the motor signals necessary for prey capture (e.g. contraction of muscles). If no mechanism compensates for such visuomotor delay, then incorrect actions will be directed towards the initially perceived position d_0 instead of the actual position d_2 (Fig. 1a). Numerous studies have shown that this latency is compensated for at the visual or motor level by extrapolating the position of the moving object (Berry et al., 1999; Borghuis & Leonardo, 2015; Johnston & Lagnado, 2015; Kerzel & Gegenfurtner, 2003; Nijhawan, 1994; Olberg, 2012; reviewed in Nijhawan & Wu, 2009). For instance, Berry et al. (1999) found that salamanders and rabbits shift their retinal image forwards along the trajectory of the moving stimulus so that the perceived position is the same as the actual one.

A robust perceptual effect, which has addressed neural delay and position extrapolation of moving objects, is the flash lag illusion. This is a visual illusion first reported in humans (Metzger, 1932) and replicated in other animals (Jancke, Erlhagen, Schöner, & Dinse, 2004; Subramaniyan, Ecker, Berens, & Tolias, 2013), wherein a briefly visible flash that is in alignment with a constantly moving stimulus is perceived to spatially lag behind the moving object (for illustration see Supplementary video S1). While the exact mechanism behind the positional lag is hotly debated (Eagleman & Sejnowski, 2000; Khoei, Masson, & Perrinet, 2017; Krekelberg & Lappe, 2001; Wojtach, Sung, Truong, & Purves,

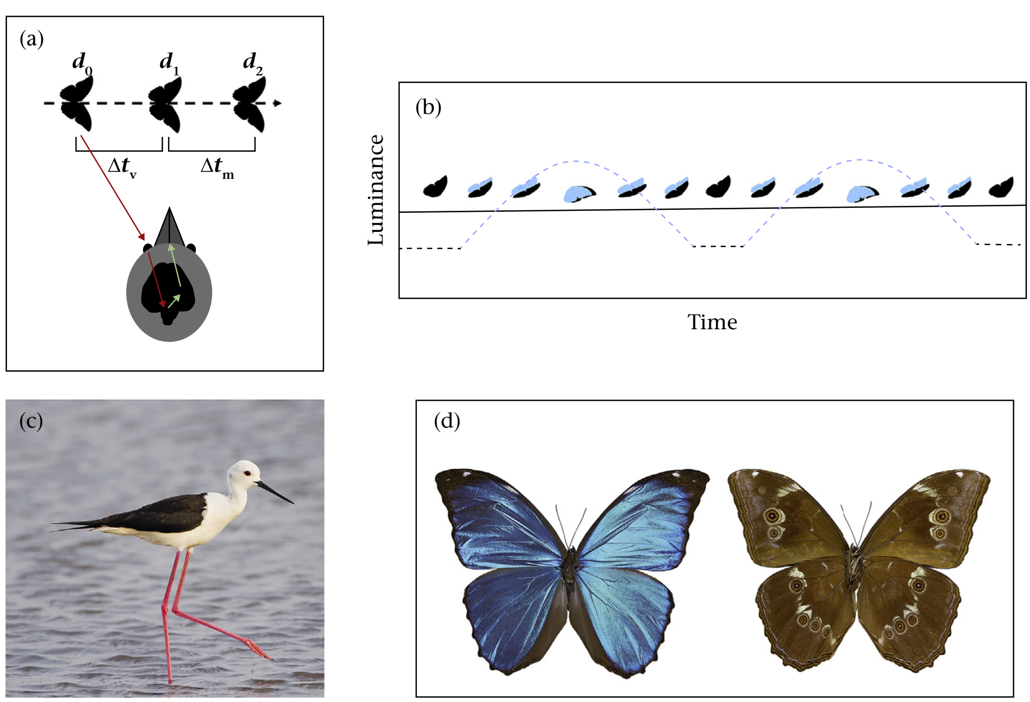

Figure 1. (a) Neural delay and the problem of position estimation of moving objects: as it takes significant time to process visual (Δt_v) and motor signals (Δt_m) necessary for prey (depicted as a butterfly) capture by a predator (depicted as a bird), if not compensated for, actions directed to the perceived position of the prey (d_0) will lag behind the true position (d_2). (b) The hypothetical plot of luminance over time (two cycles) during the flight of a butterfly with dorsoventral contrast as in (d). (c, d) Examples of animals with putative dynamic flash coloration. (c) Black-winged stilt, *Himantopus himantopus* (photo: Wikimedia Commons, J.J. Harrison) whose black wings can momentarily obscure the white body, creating a flash effect during flight. (d) Butterfly, *Morpho menelaus huebneri* (photo: Wikimedia Commons, D. Descouens) with a bright blue dorsal surface and brown ventral surface.