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Dazzle camouflage and the confusion effect: the influence of varying speed on target tracking

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The formation of groups is a common strategy to avoid predation in animals, and recent research has indicated that there may be interactions between some forms of defensive coloration, notably high-contrast 'dazzle camouflage', and one of the proposed benefits of grouping: the confusion effect. However, research into the benefits of dazzle camouflage has largely used targets moving with constant speed. This simplification may not generalize well to real animal systems, where a number of factors influence both within- and between-individual variation in speed. Departure from the speed of your neighbours in a group may be predicted to undermine the confusion effect. This is because individual speed may become a parameter through which the observer can individuate otherwise similar targets: an 'oddity effect'. However, dazzle camouflage patterns are thought to interfere with predator perception of speed and trajectory. The current experiment investigated the possibility that such patterns could ameliorate the oddity effect caused by within-group differences in prey speed. We found that variation in speed increased the ease with which participants could track targets in all conditions. However, we found no evidence that motion dazzle camouflage patterns reduced oddity effects based on this variation in speed, a result that may be informative about the mechanisms behind this form of defensive coloration. In addition, results from those conditions most similar to those of published studies replicated previous results, indicating that targets with stripes parallel to the direction of motion are harder to track, and that this pattern interacts with the confusion effect to a greater degree than background matching or orthogonal-to-motion striped patterns.

The formation of groups is a common strategy to avoid predation in animals, and recent research has indicated that there may be interactions between the benefits of grouping and those of defensive coloration. Motion dazzle camouflage consists of geometric high-contrast coloration and is hypothesized to interfere with an observer's accurate perception of speed and trajectory (Hall et al., 2016; Hogan, Cuthill, & Scott-Samuel, 2016; Hogan, Scott-Samuel, & Cuthill, 2016; Hughes, Troscianko, & Stevens, 2014; Scott-Samuel, Baddeley, Palmer, & Cuthill, 2011; Stevens, Yule, & Ruxton, 2008; Thayer, 1909). In a recent study, Hogan, Cuthill, et al. (2016) found that targets with stripes parallel to a target's direction of movement impeded the tracking of one target among many, and that this effect interacted positively with increases in group size. This indicates that some animal patterns may carry benefits for animals moving in groups. While research is increasing our understanding of how animal coloration, object tracking and movement interact, all dazzle camouflage research to date has involved targets moving at constant speed. In animal groups, it is implausible that all members would move at a perfectly constant and equal speed. This could be for a number of stochastic reasons, for instance wind, terrain or water currents, or due to individual differences in age, size, health, etc.

One benefit of group membership in animals is the confusion effect: this describes a decrease in predator attack success with increased prey group size (Krause & Ruxton, 2002; Miller, 1922). It is thought that this occurs because of an increased cognitive challenge with increasing numbers of distractors in selecting and tracking a target (Ioannou, Tosh, Neville, & Krause, 2008; Krakauer, 1995; Ruxton, Jackson, & Tosh, 2007). There is good evidence of this effect from a number of behavioural and computational experiments (see Jeschke & Tollrian, 2007 for a review). Individual variation in speed might be predicted to increase the ease with which predators can track and attack prey items in groups; this derives

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from the natural corollary of the confusion effect, the oddity effect, which suggests that targets that mismatch other group members in some way will be easier to track than ones that do not (Landeau & Terborgh, 1986). For the case of variation in speed, an individual's speed could help to identify it, in effect making the individual 'odd' and thereby undermining the confusion effect. Research into collective movement has found that animals in groups modify their behaviour, including speed, towards the group's average, especially when under high predation risk (Bode, Faria, Franks, Krause, & Wood, 2010; Herbert-Read et al., 2013; Szulkin, Dawidowicz, & Dodson, 2006). It has been argued that this evidence suggests that animals in groups act to minimize individual differences that could undermine the confusion effect. However, there are few empirical data on the influence of oddity in dynamic properties, such as speed, on predation.

Despite the recent increase in research on the possible benefits of motion dazzle camouflage (Halperin, Carmel, & Hawlena, 2016; Hogan, Scott-Samuel, et al., 2016; Hughes, Magor-Elliott, & Stevens, 2015; Murali & Kodandaramaiah, 2016; Stevens, Searle, Seymour, Marshall, & Ruxton, 2011; Stevens et al., 2008; von Helversen, Schooler, & Czienskowski, 2013), relatively little is known about the mechanisms through which high-contrast patterns may benefit moving animals. However, it has been suggested that motion dazzle camouflage may act through the manipulation of perceived speed (Hall et al., 2016; Murali & Kodandaramaiah, 2016; Scott-Samuel et al., 2011; von Helversen et al., 2013). If motion dazzle camouflage introduces inaccuracies in the observer's perception of object speed, any harm accrued through oddity in individual speed may be minimized. Hogan, Cuthill, et al.'s (2016) recent findings do not support the necessity for variation in speed for dazzle camouflage to be beneficial to animals in groups. However, in their experiment, object speed was constant, so it might have been the case that the accurate perception of speed was relatively unimportant for accurate target tracking. This also precluded target speed as a parameter to distinguish between target and distractors through the oddity effect, a strategy that may similarly rely on the accurate perception of speed. Therefore, any potential benefits to motion dazzle camouflage with respect to speed might have been overlooked.

Investigation into the influence of variation in speed on dazzle camouflage may also shed light on the mechanisms underlying it. Two leading, although not mutually exclusive, hypotheses for the mechanisms of dazzle camouflage are the aperture problem and spatiotemporal aliasing (How & Zanker, 2014; Troscianko, Benton, Lovell, Tolhurst, & Pizlo, 2009). The former arises because of the limited receptive field of individual visual motion receptors, and suggests that such receptors are unable to resolve ambiguity about the true direction of contours moving over their receptive field (Adelson & Movshon, 1982; Wuerger, Shapley, & Rubin, 1996). Spatiotemporal aliasing arguments suggest that if the speed and spatial frequency of the contours on a moving object are well matched to the temporal and spatial sensitivity of the visual motion receptors, reversal of motion may occur when one contour is mistakenly identified as another (e.g. Pakarian & Yasamy, 2003). Either or both mechanisms could act to interrupt the accurate perception of speed. However, for patterns with contours orthogonal to the direction of movement, the spatiotemporal aliasing hypothesis would predict aberrant motion signals to occur mainly in opposition to true motion (How & Zanker, 2014). Since at some point local motion signals may be integrated (Saleem, Longden, Schwyn, Krapp, & Schultz, 2012; Santer, 2013), it could be the case that such opposing motion signals would interrupt the perception of speed to a greater degree than motion signals from other patterns. Therefore, the spatiotemporal aliasing arguments could predict that the effects of the addition of variation in speed should differ between orthogonally striped and parallel striped patterns.

The current experiment aimed to address the importance of object speed in tracking by introducing conditions in which the speed of the target and distractors differed between individuals and varied over time. The inclusion of variation in speed allowed us to examine how this parameter affected the ability of the observer to track an individual in the group. Comparison of the influence of speed variation on tracking for the high-contrast targets relative to low-contrast background-matching targets indicates whether dazzle camouflage could ameliorate oddity in individual speed. Comparison of the effects of speed variation between the orthogonally and parallel striped conditions may be informative about the underlying mechanisms of dazzle camouflage. We used humans as a model species, tracking artificial targets on a screen. This approach has allowed great strides in our understanding of how perception and cognition affect visual search and predation, because of the precise control over not only stimulus properties but also 'predator' location and motivation (e.g. Ruxton et al., 2007; Stevens et al., 2011, 2008). While other factors will undoubtedly affect predation on groups in the wild, some of these being species specific, in order to control prey motion and measure its effect it is almost essential to use artificial targets under tightly controlled viewing conditions.

METHODS

A computer-driven task was created in MatLab (Mathworks, Natick, MA, U.S.A.), which followed a similar methodology to that of Hogan, Cuthill, et al. (2016) and used identical equipment. Each trial, subjects were presented with sets of 1, 10, 30 or 50 moving squares which were constrained within a central area on the screen (268 $\times$ 268 pixels). Each square was 32 $\times$ 32 pixels in size, and the direction of movement of all squares from one frame to the next can be described as a correlated random walk (see Hogan, Cuthill, et al., 2016). The participant's task was to track the movements of a predetermined target square with a mouse-controlled on-screen cursor until the end of a 5000 ms moving period. The Cartesian locations of the centre of the target square and centre of the cursor were recorded every 10 ms. The mean distance of the cursor from the target in pixels for the final 4000 ms of each trial was calculated and recorded. Participants completed six practice trials which were excluded from the analysis, followed by 336 trials in six randomly ordered blocks, one for each combination of target coloration and speed condition. The order of blocks and of trials within each block were randomized independently for each subject. There were 15 participants (nine female), who were recruited opportunistically, and each was reimbursed £7 for participation. Each gave their informed written consent in accordance with the Declaration of Helsinki, and the experiment was approved by the Ethical Committee of the Faculty of Science, University of Bristol.

In some trials the speed of the squares was varied, with a maximum speed of 300 pixels/s and a minimum of 100 pixels/s. Each square was given an initial speed determined by the addition of a random value chosen from a normal distribution with a standard deviation of 40 and a mean of 0 to the average speed of 200 pixels/s. Each frame, each square's speed was independently determined by the addition of a random value chosen from an identical distribution to the square's speed in the previous frame. This meant that squares' speeds could differ from those of other group members, and that all squares' speeds changed over time. That is, our squares were not moving as a coordinated 'herd' or 'shoal'; they were a milling swarm. This also meant that the average speed of each square over a trial was similar to that of squares that had constant speed, but the variance was much larger. In trials