



Concealment in a dynamic world: dappled light and caustics mask movement

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The environment plays a significant role in shaping the visibility of signals both to and from an organism. For example, against a static background movement is highly conspicuous, which favours staying still to optimize camouflage. However, backgrounds can also be highly dynamic, such as areas with wind-blown foliage or frequent changes in illumination. We propose that these dynamic features act as visual noise which could serve to mask otherwise conspicuous movement. Two forms of illumination change were simulated, water caustics and dappled light, to represent dynamic aquatic and terrestrial environments, respectively. When asked to capture moving prey items within the simulated scenes, human participants were significantly slower and more error prone when viewing scenes with dynamic illumination. This effect was near identical for both the aquatic and terrestrial environments. In the latter, prey item movement was also found to be masked most often when the pathway taken involved movement across the dynamic dappled areas of the scene. This could allow particularly moving prey to reduce their signal-to-noise ratio by behaviourally favouring the relative safety of environments containing dynamic features.

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Many organisms have evolved camouflage to reduce detection and subsequently evade predation (Cott, 1940; Endler, 1981; Ruxton, Sherratt, & Speed, 2004; Stevens & Merilaita, 2009; Thayer, 1909). For traditional camouflage strategies, such as background matching, this involves an organism matching (elements of) the surrounding background while remaining largely stationary (Cuthill et al., 2005; Endler, 1981, 1984; Merilaita & Stevens, 2011; Stevens & Merilaita, 2009). However, many natural backgrounds have dynamic components, not just in the physical movement of plants in wind or underwater currents (New & Peters, 2010; Peters, Hemmi, & Zeil, 2007), but also in their illumination (Endler, 1993; Endler & Théry, 1996). Here we investigated the effect on prey detection of two forms of rapid variation in the illumination: underwater caustics and dappled light through foliage.

As light passes through the spatially heterogeneous surface of water, it is diffracted in a way that diverges then converges the rays to form patterns of variable irradiance upon the substrate: these

irradiances are known as water caustic networks (Lock & Andrews, 1992; Swirski, Schechner, Herzberg, & Negahdaripour, 2009). As the water moves naturally, these networks flicker, changing in both space and time (Lock & Andrews, 1992; Swirski et al., 2009). Analogously in terrestrial environments, dappling is a consequence of light passing through foliage that, when naturally swaying with the wind, casts moving shadows onto the substrate. These shadows can be low to very high contrast (with respect to the surrounding, directly illuminated, areas) and, depending on the strength of the wind, can be anything from static to highly dynamic. Both examples of illumination variation are likely to be large sources of natural visual noise, decreasing the signal-to-noise ratio for visually oriented organisms (Merilaita, Scott-Samuel, & Cuthill, 2017), but each has an influence at a different scale. Dynamic water caustics cause changes in illumination across the whole scene (global scale), whereas dappled light has most effect on illumination locally at the margins of shade (local scale) and therefore one would expect issues with detection to be closely associated with these margins.

Visual noise, such as the movement of foliage, can alter behaviour, especially that involving signals. Ord, Peters, Clucas, and Stamps (2007) observed that the speed of vertical head-bobs and dewlap expansion displayed by territorial anole lizards, *Anolis cristatellus* and *Anolis gundlachi*, correlated strongly with the

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varying speed of wind-blown background vegetation. Similarly, Peters et al. (2007) reported that the duration of aggressive tail flicks between rival Jacky dragon lizards, *Amphibolurus muricatus*, dramatically increased when the leafy surroundings were subjected to artificially increased wind, versus ambient wind conditions; this response differentiated the tail-flicking signal from the surrounding moving foliage (Peters et al., 2007). As with all signals, there are benefits from maintaining the signal-to-noise ratio, the failure to do so here being a potential loss of territory or resources to a rival (Ord et al., 2007; Peters et al., 2007).

Whereas communication typically requires increasing the signal-to-noise ratio, traditional camouflage strategies require the opposite (Merilaita & Stevens, 2011). Therefore, just as dynamic signals must be distinct from background motion noise, dynamic cues, such as organism movement, will only go undetected if they fall within the distribution of background motion noise: in general, motion 'breaks' camouflage (Cott, 1940; Hailman, 1977; Hall, Cuthill, Baddeley, Shohet, & Scott-Samuel, 2013; Rushton, Bradshaw, & Warren, 2007; Stevens, Yule, & Ruxton, 2008; Zylinski, Osorio, & Shohet, 2009). Fleishman (1985) highlighted this phenomenon with the neotropical vine snake, *Oxybelis aeneus*, a stalking predatory species that shows rhythmic pendulous movement that coincides with the motion of wind-blown foliage. Using artificial wind, Fleishman (1985) demonstrated that *O. aeneus* consistently initiated this type of movement in response to visual cues of wind-blown vegetation and, on some occasions, to the tactile presence of wind alone. Not only do *O. aeneus* preferentially move during periods of wind-induced visual noise, but do so in a manner that mimics that noise (Fleishman, 1985, 1986). Indeed, many species use this oscillation or 'swaying' behaviour apparently to accentuate a cryptic or masquerade effect, including stick- and leaf-mimicking insects (Bian, Elgar, & Peters, 2016) and lizards of the *Chamaeleo* genus (Gans, 1967). Moreover, Ryerson (2017) found that three species of colubrid snakes preferentially use oscillating behaviour (a 'head bob') in conjunction with a dorsal pattern to mimic wind-blown grass. Indeed, these behavioural findings mirror those in psychophysics: a camouflaged stimulus is harder to detect when moving among multiple 'distractors', objects that are similar in pattern and shape to the stimulus and move at the same speed (Hall, Baddeley, Scott-Samuel, Shohet, & Cuthill, 2017; Hall et al., 2013).

Unlike the motion of the organism, the effect of dynamic illumination on concealment remains largely anecdotal, with most hypotheses addressing the putative role of dappled light in the evolution of certain camouflage patterns (Kitchener, 1991; Poulton, 1890; Thayer, 1909). Allen, Cuthill, Scott-Samuel, and Baddeley (2010) confirmed earlier comparative studies (Ortolani & Caro, 1996; Ortolani, 1999) showing that complex pelt patterns in felids, such as irregular spots, are highly associated with the closed habitats in which they live, perhaps due to the presence of dappled lighting. Further, Givnish (1990) proposed that leaf mottling in short-statured forest herbs represented a form of background-matching camouflage to hide from dichromatic herbivores on a sunlight-dappled forest floor. To our knowledge, there have been no studies of caustics conducted in relation to perception, camouflage and behaviour, although Merilaita and Stevens (2011) have previously inferred that the undulating dorsoventral contrasting coloration line of dwarf and minke whales, *Balaenoptera bonaerensis*, may be an example of background matching for 'dappled light'. In this context, the dappled light mentioned will most likely be water caustics.

We simulated both examples of dynamic illumination in computer-based experiments to investigate the extent to which they influence human perception of both moving and stationary prey items. In addition to creating fully dynamic, realistic

simulations, static examples of both illuminants were used to determine which effects are specific to movement as opposed to pattern.

METHODS

The simulated environments and subsequent experimental task were created and executed in Unreal Engine 4 (Epic Games, <https://www.unrealengine.com>). All stimuli were viewed at 40–50 cm from a gamma-corrected 15" ELO Entuitive 1525L LCD touch monitor (Elo Touch Solutions Inc., Milpitas, CA, U.S.A.), with a refresh rate of 75 Hz and a resolution of 1024 × 768 pixels.

Each trial consisted of participants being presented with one prey item within a simulated scene. The task was to search and capture, by touching, the prey item. Participants had 8 s and one opportunity to touch the prey item. There were two experiments, differing only in the simulated environment: experiment 1 used simulated dappled light upon a leaf litter background while experiment 2 used simulated water caustics upon a pebbly sea bed background (Fig. 1). Both backgrounds comprised one single image, sourced from the software's default asset package, which was tiled repeatedly to make up a background scene. We used the selected background scenes 'out of the box', with range and mean of RGB values as supplied by Unreal Engine, as these were already judged to be realistic. The target luminance was then adjusted to match the mean background luminance. The monitor settings, and thus the luminance experienced by participants, was adjusted so that there was no clipping (saturation at the lower or upper end of the luminance range). The scene covered a screen area of 1024 × 568 pixels and had a mean luminance of 88 cd/m² (experiment 1) and 97 cd/m² (experiment 2). Each scene was monochromatic and was viewed from a bird's eye perspective. Prey items could appear anywhere in one of two regions (384 × 568 pixels) within this scene (Fig. 1). The location constraint was chosen such that the item never left the screen during a moving trial. The prey item was a three-dimensional sphere with a matt surface and mean luminance equal to that of the background. When viewed from above, as in the experiment, the prey item had a circular area of 255 pixels (Fig. 1) but retained apparent depth due to the realistic projection of shadows upon a three-dimensional object. Once they appeared, prey items could either remain stationary or begin to move. Movement was fixed at a speed of 30 mm/s (3.4 degrees/s) and could occur in any direction. Appearance location, within the specified zones described earlier, and movement direction were random, picked from discrete uniform distributions using Unreal Engine's random integer generator. The simulated dappled light and water caustics were either static or dynamic (with the parameters controlling dynamism kept consistent throughout all dynamic trials). The combination of prey item and scene dynamism formed a two-by-two factorial design. Owing to the restricted locality of visual noise in trials with dappled light (the dappling was created from light passing through the leaves of virtual trees, the latter being stationary), four different zones of the environmental scene in experiment 1 were used. Each zone provided a different arrangement of trees and therefore a different arrangement of dappling. Two primary measures were recorded for each trial: outcome (hit, miss or time out) and response time to the nearest 10 ms (for hits and misses). An additional measure for experiment 1 was the pathway for moving prey items in relation to the levels of shade and open light encountered. These pathways were classified with respect to the time in direct light (versus shade) into one of five bins: 0–5%: shade only; 5–45%: mostly shade; 45–55%: shade/light mix; 55–95%: mostly light; 95–100%: light only. For further details of scene and trial generation see the Appendix. Example trial clips are available in the Supplementary Material.

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