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RESEARCH ARTICLE

Camouflage during movement in the European cuttlefish (*Sepia officinalis*)

Noam Josef^{1,2,*}, Igal Berenshtein^{1,2}, Graziano Fiorito³, António V. Sykes⁴ and Nadav Shashar¹

ABSTRACT

A moving object is considered conspicuous because of the movement itself. When moving from one background to another, even dynamic camouflage experts such as cephalopods should sacrifice their extraordinary camouflage. Therefore, minimizing detection at this stage is crucial and highly beneficial. In this study, we describe a background-matching mechanism during movement, which aids the cuttlefish to downplay its presence throughout movement. *In situ* behavioural experiments using video and image analysis, revealed a delayed, sigmoidal, colour-changing mechanism during movement of *Sepia officinalis* across uniform black and grey backgrounds. This is a first important step in understanding dynamic camouflage during movement, and this new behavioural mechanism may be incorporated and applied to any dynamic camouflaging animal or man-made system on the move.

KEY WORDS: Animal behaviour, Cephalopods, Movement camouflage, Dynamic camouflage, Background matching, Common cuttlefish, Chromatophores

INTRODUCTION

Crypsis is a common behavioural–morphological adaptation aimed at minimizing detection by predators or prey (Caro, 2005a,b; Ruxton et al., 2004). Visually active organisms are skilled at detecting movement, which often indicates the existence of a potential danger or of an object of interest (Cronin et al., 2014; Land and Nilsson, 2012). As a result, cryptic animals tend to keep still in various situations (Cott, 1940; Poulton, 1890; Zhang and Richardson, 2007), such as a prey that ‘freezes’ upon detecting a distant predator (Broom, 2005; Eilam, 2005) and ‘sit-and-wait’ or ambush predators, which do not move while waiting for their prey (Thery, 2004). Therefore, camouflage is traditionally linked to motionlessness, making it a widespread example of coevolution between behaviour and morphology (Ioannou and Krause, 2009). This linkage has led to the common belief that it is difficult to move and stay camouflaged at the same time. The obvious advantage of camouflaging during movement is enabling the approach of a predator to a prey without it noticing. This and other advantages have led to the development of several strategies that allow animals to maintain at least partial camouflage and remain undetected while moving. There seem to be three schemes in which this may occur: motion signal minimization, optic flow mimicry and motion

disruption (Troschianko et al., 2009). Camouflage through motion signal minimization is associated with the prevention of low-level detectors indicating motion activity. Camouflage through optic flow mimicry is associated with an attempt to mimic the background or surrounding motion so that, although the motion is detected, it does not provide a cue for segmentation. Motion disruption involves a breaking or misrepresentation of motion cues to distort the perception of that motion. Dragonflies and hoverflies, for example, perform ‘motion camouflage’ by keeping their narrow cross-section faced towards the target even when flying sideways in relation to it (Mizutani et al., 2003). The observation that certain unrelated species resemble one another has long been reported (Darwin and Wallace, 1958; Ruxton et al., 2004), describing strategies such as mimicry, stealth and deceptive resemblance (Cott, 1940; Randall, 2005), but evidence of their use and effectiveness in the animal kingdom is lacking.

Cephalopods are considered masters of rapid adaptive camouflage. Using their multi-layered skin and neural-controlled chromatophores they can change colour, pattern, texture and reflectance in a fraction of a second (Barbosa et al., 2012; Hanlon et al., 2009; Marshall and Messenger, 1996; Mäthger and Hanlon, 2007; Mäthger et al., 2006, 2009; Messenger, 1974; Zylinski and Johnsen, 2011), making them hard to detect by both prey and predator. The cephalopods’ camouflage has been investigated through qualitative and quantitative experiments, pattern catalogues and behavioural studies (Barbosa et al., 2012; Borrelli et al., 2006; Darmaillacq et al., 2014; Josef et al., 2012; Kelman et al., 2008; Zylinski et al., 2011). Recent works have shown that cephalopods can use camouflage to minimize detection when moving over different background patterns (Hanlon et al., 1999; Shohet et al., 2006; Zylinski et al., 2009). Some octopuses perform the ‘moving rock’ manoeuvre (Hanlon et al., 2008, 1999) in which they mimic a rock as they move, whereas some mimic other fish as they swim (Norman et al., 2001). Staudinger et al. (2013) also show that cuttlefishes adapt their cryptic behaviour according to the presence of various teleost predators. Multiple camouflaging techniques and anti-predator behaviours, such as the ‘moving rock’ are synergistically combined to yield the best cryptic result (Norman et al., 2001; Stevens et al., 2011). However, the question of camouflage and background matching during motion remains open. In other words, how can a cuttlefish motion be camouflaged and which of the mentioned schemes does it use? In the current study, we examined the cuttlefish’s ability to alter their mantle reflectance while crossing between two highly contrasted backgrounds.

Theoretically speaking, any dynamic camouflager facing a change in background may choose to match its background from selection of schemes. A camouflaging cuttlefish facing a change in background may choose to modify its mantle pattern either instantaneously or gradually (Fig. 1). In the first approach (Fig. 1A), the animal does not change its colour and remains

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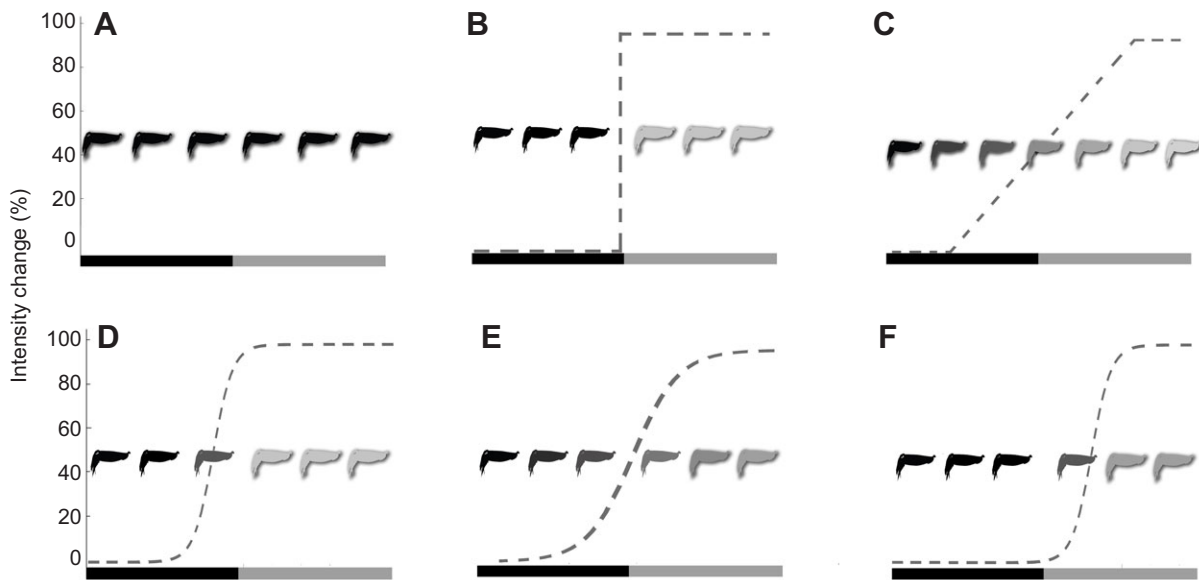


Fig. 1. Theoretical illustration of a cuttlefish swimming from a black to a grey background, showing possible camouflage schemes. (A) An animal may retain its body reflectance throughout its course, forgoing camouflage altogether. (B) An animal may change its reflectance in an instantaneous step-like manner, with very short transition between the two displays. (C) It may linearly alter its body pattern – in this case its reflectance. The gradual change can be expressed as sigmoidal or by other functions. Any animal gradually changing its reflectance may choose to (D) start and finish the change in advance – matching its reflectance prior to the upcoming background, (E) start changing its mantle reflectance in advance, while finishing the adjustment well after crossing to the upcoming background, or (F) perform the entire reflectance change, after crossing to the new background.

cryptic as long as it is moving over the first background. Once moving onto a new background, the animal instantaneously becomes highly conspicuous. A step-like change (Fig. 1B) is achievable, assuming the animal operates a dynamic and very quick camouflage, as many cephalopods do. Clearly, instantly matching the background is the best camouflage, yet physiological constraints drive animals to find alternative approaches. In a gradual approach (Fig. 1C–F), an animal modifies its reflectance over a certain distance and time. Such an approach moderates the change in the observer's field of view, at the cost of becoming partially conspicuous over both backgrounds. Finally, a gradual

modification may also occur in the rate of change and in the position in which it takes place, as change can start and end before (Fig. 1D), during (Fig. 1E) or well after (Fig. 1F), passing from one background to the other. As is illustrated in Fig. 1, camouflage during motion includes in many cases (all but Fig. 1B) a period of time in which the animal may be conspicuous in relation to the background. This potential mismatching is considered another reason for avoiding camouflage during motion. In this study, we study the time-related process of such camouflage during motion.

MATERIALS AND METHODS

Animals

Eight naive common European cuttlefish (*Sepia officinalis* Linnaeus 1758), mantle size of 7.2–12.3 cm, were collected from the Gulf of Naples, Italy and were held in separate tanks with running seawater at the Stazione Zoologica Anton Dohrn, in Italy, for 2 days of acclimation. The cuttlefish were fed with live crabs, and maintained under a 12 h:12 h dark:light regime. When experiments ended, all animals were returned to the Gulf of Naples. Animal maintenance and experimentation were in compliance with EU directive 2010/63 on the protection of animals used for scientific purposes, and following the recommendations of the 3Rs (Fiorito et al., 2014).

Experimental design

Experiments were conducted in a secluded room, with a dividing curtain surrounding the set-up to minimize visual cues and external stressors. An elongated tank (200×40 cm, water level 45 cm) was coloured in a uniform 18% reflectance grey; the reflectance throughout this article is based on a standard 18% grey card, photographed inside the elongated tank, where 0 to 100% represents black and white, respectively. In the dichromic pattern, a dark section (64×40 cm, average reflectance 6±1) at the centre of the bottom of the tank was added (Fig. 2A). Since tactile information is a potential camouflage signal, all textures were uniform and smooth. Illumination across the tank was fairly homogeneous (350±5 lx, measured with a PeakTech 5025 light meter), to avoid shaded areas or light reflections. The water in the experimental tank was replaced prior to each trial.



Fig. 2. Experimental set-up. (A) Experimental tank with a dichromic pattern – uniform 18% grey to uniform black then back to uniform 18% grey – on the bottom. (B) A cuttlefish mantle showing the 1000 pixel rectangular sample area (yellow).

Testing procedure

Animals were tested separately. After being placed at one end of the experimental tank each animal was left to settle for at least 5 min. We then waited until two conditions were met: (1) The animal remained motionless on one side of the tank; (2) The body colour became uniform and generally matched the grey background, and remained stable for at least 2 min. The animals were then observed and recorded using video as they moved in the tank, mostly crossing it along its length. If the animals did not move within 15 min of observation, they were motivated to cross the tank either by simply standing at one end of the tank, or by providing a shelter at the opposite side of the tank. Under no circumstances were the animals scared or strongly motivated, to minimize stress. Both in control and dichromic conditions, animals were recorded crossing the tank, mantle first, from one side to the other (hereafter: ‘full-cross’). Swimming mantle-first did not affect the results, because cuttlefish possess both anterior and posterior binocular visual fields (Watanuki et al., 2000), which allow them to clearly see and plan their route while swimming forwards or backwards. In the control situation, a full crossing of the tank provided information on the animals’ changes in body colours during motion, when the background remained constant, while the dichromic pattern involved one grey-to-black and one black-to-grey background transition. Two ‘full-crossings’ (back and forth) were recorded for each of the 8 animals, resulting in 16 full crossings and 32 background transitions: 16 grey-to-black and 16 black-to-grey. Because of technical limitations (one ink cloud occluding an animal’s position and one fast-jetting animal), two background changes were excluded from the analysis, consequently leaving 30 background changes. In the control background, each of the eight animals swam across the tank once. Experiments were run during the day (09:00–17:00 h).

Data acquisition

Movements of the animals were recorded by a SONY HDR-CX110 digital video camera, mounted vertically above the tank, providing a top-down view. The camera’s field of view covered the entire width and 70% of the tank’s length, filming 1440×1080 pixels video files. To achieve high-resolution frames for analysis, the camera was set so it photographed only 140 cm out of the 200 cm tank length. Hence, we have no record of the last 30 cm at each end of the elongated tank.

Data analysis

Cuttlefish possess a single, mid-wavelength visual pigment, making them essentially colour blind (Hanlon and Messenger, 1998; Marshall and Messenger, 1996; Mäthger et al., 2006). Moreover, most of the changes in the background and the cuttlefish display are monochromatic in nature, so we chose to look only at changes in reflectance and not in colour. Therefore, videos were grey-scale transformed, using the green channel alone. Videos were analysed using a designated MATLAB code (Matlab v7.14, MathWorks, Natick, MA, USA). The outline of the code is: (1) loading a video file, (2) transforming each frame into a grey-scale intensity image, (3) balancing each frame according to the 18% grey standard, (4) manually tracking the animal in 1/10 of a second intervals, and (5) measuring the animal’s mantle reflectance (an average of the mantle section), velocity and relative position in relation to the next background. Cuttlefish can present three types of body patterns: uniform, mottle and disruptive (Chiao et al., 2007; Cott, 1940; Hanlon and Messenger, 1998). In our set-up, because of the uniform background, the animals elicited a uniform body pattern in all cases. Therefore, we used the average values of 1000 (40×25) pixels surrounding the centre of the mantle (Fig. 2D). To characterize the trends in each case, we extracted and analysed each section separately, paying special attention to the start and end points of each transition. Transition start and ending, were determined by manually selecting points which marked the beginning or ending of drastic change in reflectance. A starting or ending point was only chosen if the trend was maintained for at least three consecutive measurements. Once we marked the beginning and ending points of each session, we calculated the ‘time before crossing’ (TBC) and the ‘time post crossing’ (TPC). During the short reflectance-changing sections animals swam at a rather constant

speed (average acceleration/deceleration $0.022\pm 0.01\text{ m s}^{-2}$). Therefore, in this set-up, time and distance are linearly related.

Since each animal began and completed their transitions in various locations and at various reflectance values, we normalized our results to the entire transition change (100%). The percentage was calculated as the portion of the entire change in place and in reflectance.

The percentage we used in Fig. 5 represents the change during the entire transformation. Meaning that the *y*-axis shows the percentage change of the whole reflectance change, whereas the *x*-axis is the percentage displacement of the total animal movement during the transition. After

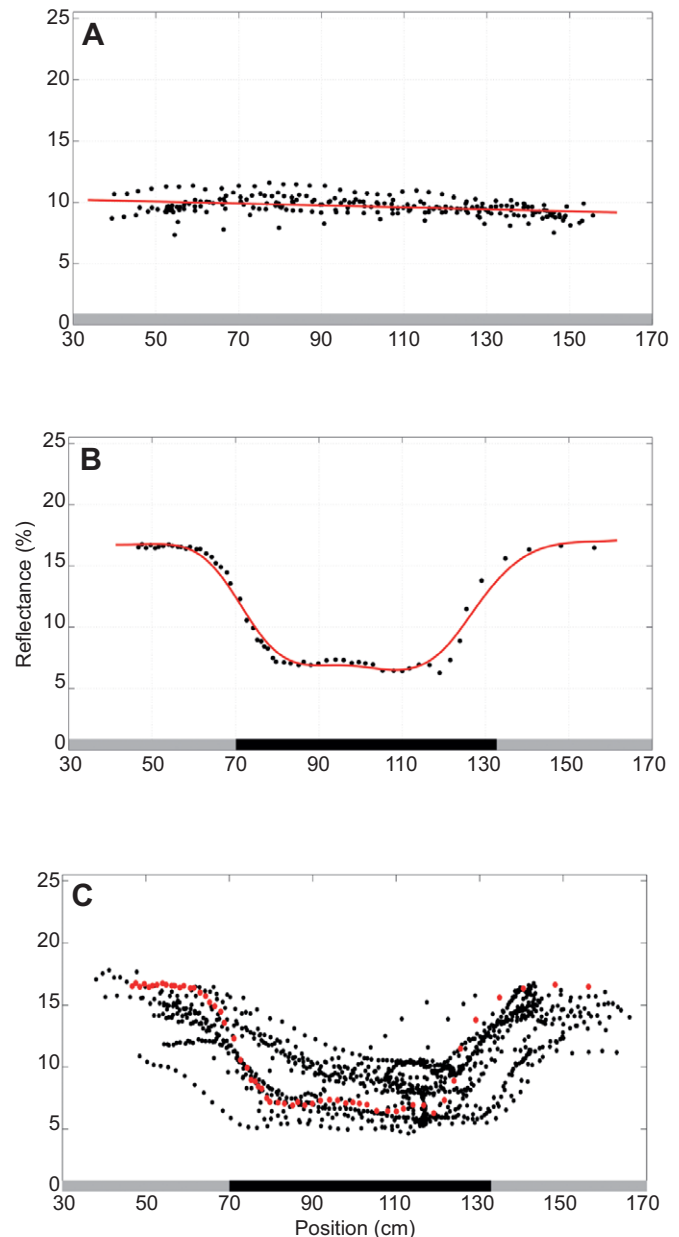


Fig. 3. Body reflectance of cuttlefish as they cross the experimental tank. (A) When crossing a control grey tank, none of the eight cuttlefish drastically changed its reflectance. The near-horizontal linear regression line demonstrates the overall constant reflectance. (B) Mantle reflectance of a single animal swimming from left to right over a changing background, matching its mantle reflectance to the background as it swims across the tank. The smooth trend line (smoothing spline parameter: 1.05×10^{-5}) demonstrates the reflectance matching along its path. (C) All runs ($N=30$) superimposed, illustrating the persistent reflectance-matching behaviour over a changing background. The red dots describe a single animal reflectance, as in B.

plotting the normalized transitions (Fig. 5), we used the Matlab Curve Fitting Tool to fit the Gaussian trend line (using two terms). To eliminate possible learning and habituating factors, we analysed the first and second transitions independently and compared them. Validating a normal distribution (using the Kolmogorov–Smirnov test), a paired-sample *t*-test with 95% confidence interval was performed to check for differences in behaviour between the first and the second transition. No significant differences were found between the first and second transition in terms of average velocity, mean change duration and total reflectance ($P=0.028$,

0.034, 0.021, respectively). Therefore, data from both transitions were combined in the analysis.

To measure the reflectance uniformity within the mantle, we divided the mantle length into 10 segments, where 1 is the posterior and 10 is the anterior side. Each segment was measured for its average reflectance, during the cuttlefish swim over changing backgrounds. Then, we tested the 10 segments using a two-way ANOVA to verify whether the mantle changed in a uniform or a gradual manner.

RESULTS

Eight naive common European cuttlefish were placed in an elongated tank with either a control pattern (complete 18% reflectance grey), or a dichromic pattern composed of three areas: grey, black and grey again (3% black and 18% grey; Fig. 2A). The swimming cuttlefish were tracked and their mantle reflectance was continuously monitored. In the uniform grey control tank, all eight animals maintained their overall light and uniform body coloration, matching the background throughout their movement (Fig. 3A). However, when swimming over the changing background, all animals became darker as they swam over the dark section and then lighter as they moved back to the grey section (Fig. 3B,C).

In all cases, the cuttlefish's mantle changed simultaneously, without having the front or back half of the animal showing different reflectance as the animal passed the boundary. Comparison of the different features of movement and camouflage did not reveal any difference between crossing from a grey to a black background versus crossing from a black to a grey background. For example, the mean reflectance change, change duration and TBC versus TPC were not significantly different between the two scenarios (Wilcoxon rank test with 95% confidence interval, $P=0.1$, $P=0.29$, $P=0.18$, respectively). Therefore, from here on, we only address reflectance change behaviour without distinguishing whether it was from grey to black or from black to grey. An example of such reflectance change can be found in Fig. 4. TBC, TPC and total time of change did not correlate to the average velocity during transition (pair-wise correlation test coefficients of 0.216, 0.325 and 0.42, respectively).

The reflectance values within different mantle segments were measured. Measuring frame by frame indicated a uniform change along the animal's axis, $F_{9,220}=53.8$, $P=0.002$, with no gradual change recorded between the different segments, indicating that the entire mantle changed simultaneously (Fig. 5).

Animals varied in the levels and duration of reflectance changes. Normalizing each transition to the animal's maximal reflectance and total transition duration, revealed a sigmoidal trend in the reflectance change of all animals (Fig. 6). Each of the 30 transitions could be fitted with a sigmoidal curve, with an r^2 value no lower than 0.85 (see example in Fig. 6A).

The mean duration of reflectance changes was 1.59 ± 0.96 s. In 27 out of the 30 transitions, animals started changing their body reflectance before they crossed the background boundary (Fig. 7). However, the greatest part of the changing process took place after crossing onto the new background. The TBC varied between individuals (mean TBC of 0.47 ± 0.58 s), corresponding to ~30% of the total time of change. However, most of the transition occurred after switching backgrounds (TBC versus TPC, $P\ll 0.01$, $N=30$, Wilcoxon rank test with 95% confidence interval).

DISCUSSION

We present here, for the first time in the study of animal camouflage, characteristics of background matching during motion. Cuttlefishes alter their mantle reflectance and match a changing background, maximizing crypsis while still on the move

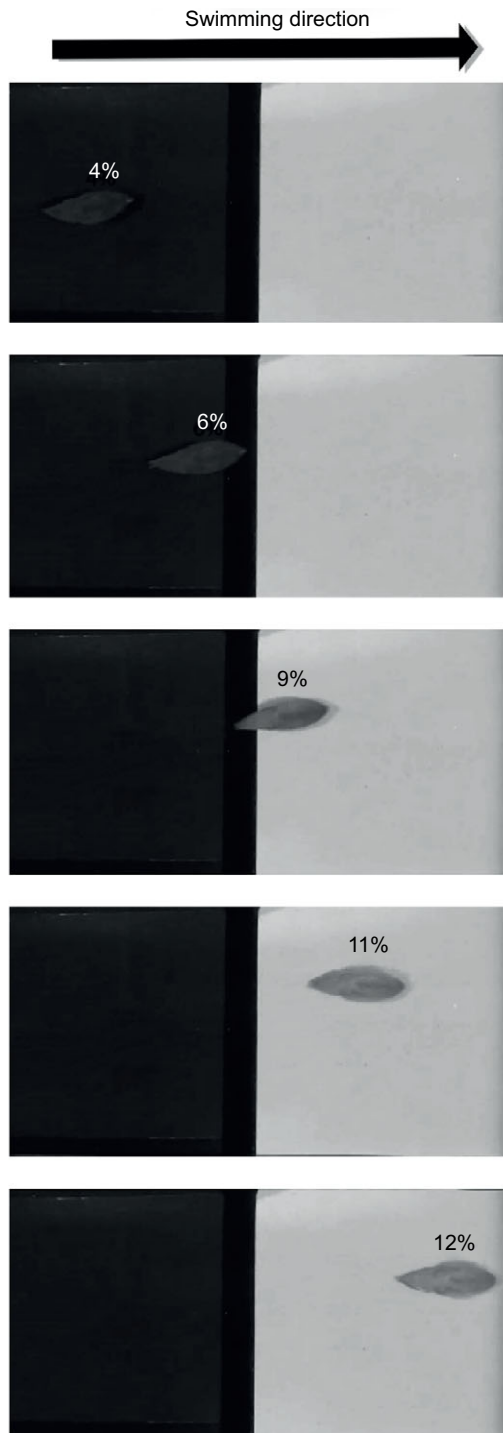


Fig. 4. A cuttlefish matching its background as it swims from a black to a grey background. The white number represents the mean mantle reflectance value as it moves.

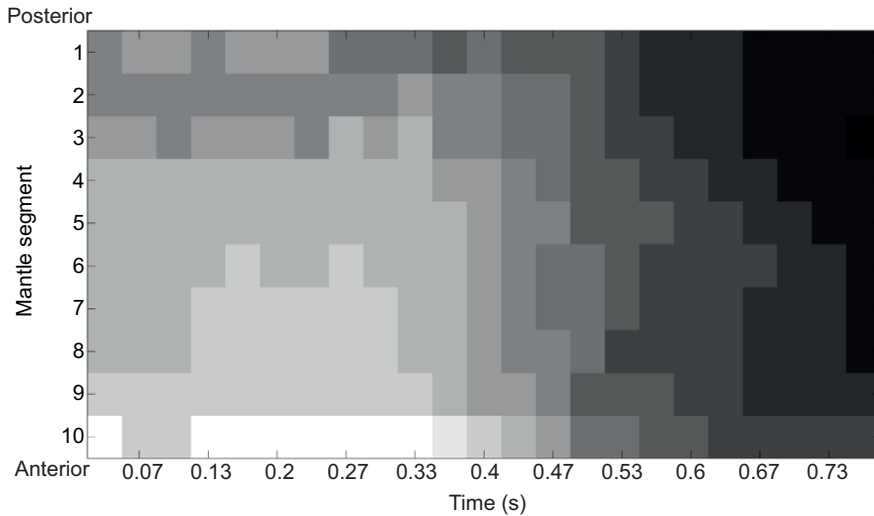


Fig. 5. A representative reflectance map of the 10 mantle segments during a change in background. Each mantle segment changed reflectance almost simultaneously, with no evidence of a gradual change.

(Fig. 4, Movie 1). Our results demonstrate that mantle reflectance varies in a sigmoidal manner as animals start their change in advance of, but finish well after, crossing to the new background (Fig. 1E).

Dynamic camouflage is a multidimensional task. Matching the brightness, texture and pattern to different backgrounds requires an advanced visual system, processing capabilities and proper skin physiology, which may include specific photoreceptors (Ramirez and Oakley, 2015). Changing colour and reflectance while chasing a prey or hiding from a predator requires the cephalopod to possess a high level of visual information processing and the control of skin

chromatophores and irridophores, without interfering with the activity it is engaged in.

It should be noted that background matching should fit the visual system of the predators and not necessarily that of the cuttlefish. In this experiment, we examined background matching on black and grey patterns, which should be similar to most types of observers. Yet a detailed study as to how potential predators view cephalopod camouflage has yet to be performed (Siddiqi et al., 2004; Stuart-Fox et al., 2008). Preliminary observations, as well as discussions with Prof. Roger T. Hanlon, suggest that octopuses may also be able to camouflage during motion. This, along with the current study, brings into focus the need for a deeper understanding of camouflage during movement in various organisms, its limitations, and the controlling mechanisms.

A moving camouflaging animal may change its properties in many ways. Our results indicate that in most cases, the cuttlefish were anticipating the upcoming background (Fig. 7) and changed their reflectance in a sigmoidal fashion (Fig. 6). To achieve this, an animal has to estimate in advance (1) the time it reaches the new background and (2) the reflectance of the approaching background. Following the optic flow mimicry scheme, such prediction and early response are beneficial, together with the gradual change in reflectance, in order to avoid unwelcome attention from nearby

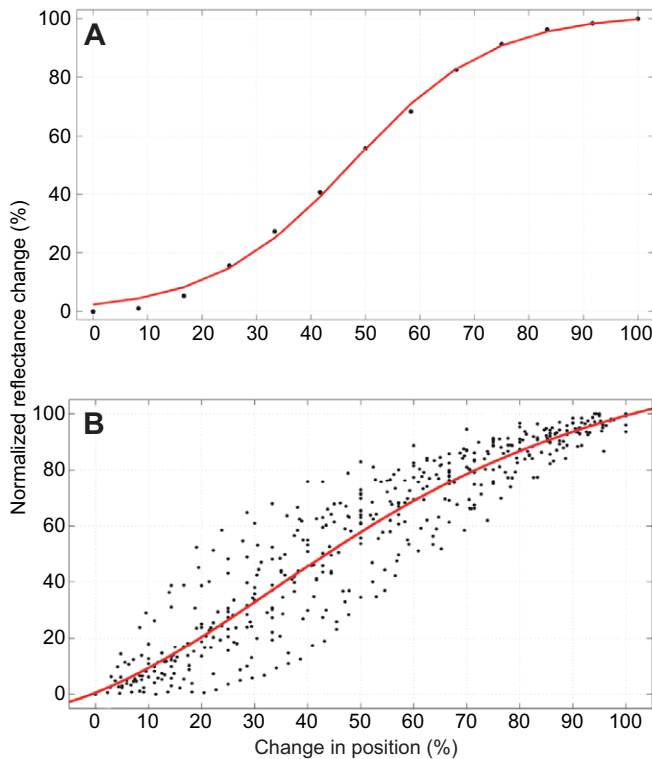


Fig. 6. Normalized reflectance transition of cuttlefishes as they crossed from one background to another. (A) A single transition event, displaying a sigmoidal trend, which was consistent for all transitions ($r^2=0.992$). (B) All 30 background-crossing episodes. The red sigmoidal fit is the averaged overall Gaussian sigmoidal trend, corresponding to the single transition in A ($r^2=0.9$).

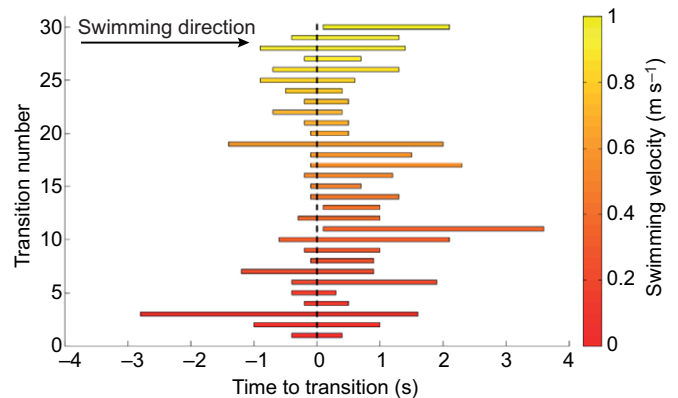


Fig. 7. The duration and timing of each reflectance change relative to the background transition line. Swimming from left to right, the bars represent the time during which the animal changed its body reflectance. '0' is the set time of crossing between backgrounds. Coloured bars represent the average velocity of the animals during this period.

observers. In primates and cats, neurons sensitive to motion are found in the primary visual cortex (Hubel and Wiesel, 1959, 1962); in other species (i.e. rabbits and frogs), they may be found within the retinal processing system (Barlow et al., 1964; Finkelstein and Grusser, 1965). The high sensitivity of many animals to drastic changes in the visual field (Borst and Egelhaaf, 1989; reviewed in Hildreth and Koch, 1987), may alert bystanders and break crypsis. In an effort to minimize such drastic changes, camouflaged organisms tend to remain motionless or move as slowly as possible. These behaviours, together with our current results, raise the question of whether there is a speed limit at which all camouflage fails and then there is a switch to other evasive manoeuvres.

In our case, no correlation was found between camouflage properties and the animal's velocity, which indicates a highly dynamic mechanism, regulating the general appearance of the animal during the phase of reflectance change. The dynamics of the change, following a general sigmoidal change versus time relationship, suggests an early slow phase, possibly showing the end of detection of the approaching background, a rapid phase and a slow fine-tuning phase. This raises the question of whether dynamic camouflage is completely cognitive or whether it consists of a passive/reflex-like component. Such a mechanism may derive from the requirement to complete the transition in the shortest time possible.

We would like to stress that in the wild, a clear transition between two uniform backgrounds is rare, whereas most natural scenarios include a blending phase comprising complex backgrounds that affect each other. This reason alone may drive the development of such a gradual and sigmoidal trend in reflectance change. In Fig. 5B, it seems that there is a potential biological constraint for the reflectance change, suggesting upper and lower limitations to the animal's background matching. Such limitations might represent the animal's point of view, chromatophore change rate, processing time or a combination of all three.

Although all animals changed their reflectance while moving between the two uniform backgrounds, in several cases the overall match in reflectance was partial and limited (Michelson contrast ranged between 0.15 and 0.76). This is possibly due to biological and physical constraints when matching an artificial uniform background (i.e. the cuttlefish could produce neither a perfectly uniform 18% grey nor a 3% black pattern). Since the uniform backgrounds elicited a uniform display in all the cuttlefish, we address the overall reflectance of the mantle without dividing it into the common skin components (Barbosa et al., 2007; Hanlon and Messenger, 1988). An interesting continuum to this study would be to further investigate mantle reflectance change while moving over complex backgrounds.

Changing one's reflectance to match a changing background provides a period of time during which crypsis is compromised, at least to some extent. Since camouflage is sacrificed, one has to choose when to do so: before or after changing backgrounds. Each timing preference entails slightly different benefits and drawbacks. Since the tested animals performed most of the change process after crossing onto the new background, we suggest that in most cases, minimizing detection over the current background while compromising crypsis over the next is favoured. Although it is outside the scope of this manuscript, these results might also suggest that dynamic camouflage behaviour requires time to integrate visual input and respond accordingly.

Static camouflage is a widespread adaptation strategy, known in many animal taxa. Background matching via colour changing is a

widespread phenomenon appearing on various time scales, from several months, to weeks, minutes and even seconds [e.g. rock ptarmigan (*Lagopus muta*), spider crab (*Misumena vatia*), common chameleon (*Chamaeleo chamaeleon*) and snubnose emperor (*Lethrinus borbonicus*), respectively]. Given the benefits of dynamic camouflage, one would expect it to have developed many times throughout the evolution process. Yet, few species show dynamic camouflage capabilities.

The fast and adaptive camouflaging system of cephalopods enables colour change in less than a second (Hanlon et al., 2011). Therefore, these rapidly camouflaging animals face an unprecedented dual challenge – staying as cryptic as possible during motion and altering their colour in a manner that will not attract undesired attention. As far as we know, the described camouflaging scheme is the first to address such a challenge. Cuttlefish anticipate the upcoming background, start changing colour in advance and change it in a sigmoidal manner. This type of camouflaging strategy may be beneficial for other fast-moving animals or man-made objects trying to maintain crypsis while moving. When designing a camouflaging mechanism or algorithms, one should take into consideration all possible background-matching schemes, including when and where should the modification take place. Our current study emphasises the importance of anticipation of background matching and gradual colour change in dynamic camouflaging, which may also apply to advanced dynamic camouflaging technologies. While we stress the importance and application of studying dynamically changing patterns, automated camouflage pattern quantification and classification are not yet fully understood and is still undergoing many changes. Therefore, we started by studying uniform backgrounds and analysing the mechanism of background matching using well-defined factors and descriptors. We expect that further in-depth studies may include the study of changing patterns during motion using more complex backgrounds.

In conclusion, we described here the camouflaging behaviour of a moving cuttlefish (*Sepia officinalis*) when crossing from one uniform background to another. Following the optic flow mimicry scheme and minimizing changes in the optic flow, the cuttlefish altered their mantle's reflectance in a sigmoidal fashion, while performing most of the mantle matching well after crossing onto the new background (as described in Fig. 1F). The cuttlefish have proved to be an exciting model for investigating evolutionary and development processes in general (Bassaglia et al., 2013) and camouflage and motion in particular. Indeed, our analysis is applicable to a broader examination of camouflage patterning and may be used for both hypothetical and practical applications in the development of man-made dynamic camouflage systems (Yu et al., 2014). In a moving yet camouflaging system, one should take into consideration that camouflage is a compromise to some extent and uses the most effective scheme of background matching available within its physio-mechanical constraints. We suggest that even when given a fast-changing dynamic mechanism, an advantage would arise from a gradual change, preferably over the new background. Future studies may include quantification of shifts in body patterns and examination of the use of papillae during movement.

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experiments performed in this study complied with the Italian National Legislation for animal experiments and with EU directive 2010/63 on the protection of animals used for scientific purposes (Fiorito et al., 2014; Smith et al., 2013).

Competing interests

The authors declare no competing or financial interests.

Author contributions

N.J.: experimental design, performed experiments, data analysis and manuscript preparation. I.B.: data analysis and edited the manuscript. G.F. and A.V.S.: experimental design and data acquisition. N.S.: experimental design, performed experiments and manuscript preparation.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.122481/-DC1>

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