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In the corner of the eye: camouflaging motion in the peripheral visual field

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Original submission:	20 June 2019
1st revised submission:	30 October 2019
2nd revised submission:	9 December 2019
Final acceptance:	10 December 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2019-1457.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Acceptable

General interest: Is the paper of sufficient general interest?
Acceptable

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is an interesting paper that describes a well-designed and executed experimental analysis of the effects of a small subset of visual motion parameters viewed in the visual periphery on subsequent fixation and localization of the moving stimulus. Human subjects gaze directly forward, and then observe a stimulus square moving briefly in their periphery (the object moves and disappears) and they are then challenged to click on the location where it was last seen. The pattern of the moving dot and its velocity and duration are varied, and localization accuracy is determined.

The experiment seems to be well carried out and analyzed and, for the most part, reasonable conclusions are drawn. A weakness of the paper is that it attempts to present this as an ecologically-relevant test of the processes underlying motion detection by visually hunting prey (or prey looking out for visually hunting predators). While there are some useful conclusions in this regard, the insights gained are not as useful or general as suggested.

As the authors indicate, in many predatory species, the spatial resolution of the visual periphery is many times lower than that of the center. The peripheral visual field is often served by motion-sensitive neurons with rather large receptive fields. Such neural circuits are extremely effective at detecting even very subtle motion (and often its direction), and they will often drive reflex shifts of the eye to place the moving image close to the center of the visual field. The moving object may then be detected by its shape (or color or pattern etc.) or, as is often the case with visual hunters that depend on motion, subsequent motion will reveal the precise location of the prey and elicit a strike. Given the relatively low acuity of the periphery, and large size of the receptive fields of the motion sensitive neurons, it does not seem that the system has evolved for precise localization of motion perceived in the periphery. Rather, there is two-stage process -- place the image somewhere in the higher acuity region of the retina, and then respond to subsequent motion (or spatial characteristics) when it occurs within this area of higher acuity. Thus a critical of role of the visual periphery is to detect whether, and roughly where, motion has occurred. Precise localization of the motion is probably not a critical first step.

This paper is presented as testing the effects of motion parameters on the analysis of detection and localization. However, in fact, there does not seem to be any test of how motion parameters impact detection: the viewers are required to attempt to localize the moving stimulus in every trial, so there is no test of detection. This limits the utility of the study, because it is not clear that precise localization of a moving target detected in the periphery is important in many predator-prey interactions.

If the authors could explain conditions (or provide examples) under which precise initial localization is critical, and if they refocus the manuscript on this process itself it would be considerably strengthened.

I would also point out that there is a body of literature on the role of motion parameters and surface parameters (e.g. luminance contrast, pattern contrast, chromatic contrast) on detection of moving objects. It is well-established, for example that most motion perception relies on luminance contrast, so this result is interesting, but not novel. It would be worth reviewing some of this literature because some of the conclusions reached in this paper are at odds with these earlier studies. For example, short duration, middle amplitude, high velocity, abrupt movements have been shown to be optimally effective at eliciting visual attention. This seems to contradict the results here. Part of the issue may well lie in differences in the experimental task (e.g. localization versus initial detection), and in details such as the range of amplitudes considered, and whether or not the moving target remains visible or disappears.

Specific comments:

Line 9. This is true of some predators but not all.

Line 13-14. "The same logic applies…". I'm not sure I agree with this. Precise location and detection are not identical problems. A neural circuit with a large receptive field can be superb for detection of motion, but not so good for localization. These really are two distinct processes.

Line 23-24. It is unclear what is meant by this statement. Are you referring to a non-moving target?

Line 25. This is true in some, but not all, animal species.

Line 40. This is true, although there are animals such as stick insects, chameleons and vine snakes that use plant-like motion as a form of camouflage.

Line 44. What you refer to as "motion dazzle" is not really tested in this experiment. "Motion dazzle" refers to the example where an animal flashes a shiny surface that startles or overwhelms the predator's visual system. There is no way that the stimulus described in this experiment would have this effect on the subjects. The experiments described in this paper test something closer to the "flash concealment hypothesis" (see Hasson 1991 Trends Ecol. Evol.,6, 325–329).

Line 58. Duration and speed are not the only key parameters of transient motion, and they may not be the most important. I'm not suggesting it is invalid to examine these parameters, but it is misleading to suggest that they are the only important factors. In theoretical (and experimental studies) of motion detection, amplitude of motion across the retina has also proven to be very important. It is, of course, awkward to include this in the analysis because it co-varies with the other two parameters. Never-the-less, motion detection circuits tend to be tuned to respond optimally to certain motion amplitudes. Obviously minimum resolution is a critical parameter for

motion detection, so amplitude cannot simply be ignored. Further, abruptness of movement (possibly even acceleration) has been shown to be a critical parameter.

Line 59. It does not seem to me that the stimulus employed here represents a startle display. The second idea – what I have called "flash-concealment" above – is closer to what is being tested. This is not like the abrupt flash of a moth or butterfly wings, but more similar to tail-wagging or head-bob displays given by some lizards right before they move quickly into hiding.

Line 68. It is not clear to me how detection is tested in this experiment.

Line 107. This stimulus does not, to me, seem to represent the definition of a deimatic display. I doubt it has any startle or distraction effect on the viewer. As I suggest above, I think it fits better with the idea of a "flash-conealment" type display. Rather than interfere with the function of the nervous system, it is hypothesized to elicit a strong attention response that interferes with the ability to track the motion that follows immediately after it. "Deimatic" is a rather obscure term that most will be unfamiliar with (I had to look it up), and it does not apply particularly well in this case.

Lines 110-127. I do not see where "detection" is tested in this methodology. In every case the subject is ultimately "informed" of which side the motion occurred, and then tries to locate it. Where is the ability to detect, or not detect the stimulus tested?

Line 143. What is the "central screen?" This was not mentioned in the methods.

Line 145. If "response time" results are not presented in the main body of the paper, it should not really be raised in the discussion.

Line 190. I do not see how these experiments lead to any conclusions about "detecton." Only localization has been tested. This is not a trivial point, as I discuss later.

Line 191 – discuss this conclusion with reference to other work, the role of the visual periphery in motion detection and the ecological relevance of the work.

Line 192 – the conclusion that a luminance matched target is more difficult for motion perception is very well established.

Line 194-195. It is not really useful to discuss response times or directional errors in the discussion since no results concerning response times are included in the "results section" of the paper.

Lines 205-208. I'm skeptical about this conclusion. Motion sensitive predators will tend to fixate in the approximate area of the initial motion, then wait for the next movement to occur, at which point they can fixate much more effectively because the higher resolution portion of the visual field is likely to cover the location of the prey. Unless an animal waits until the predator shifts its gaze again, intermittent movement will not be of much help. In fact I have observed a number of predation events involving highly motion sensitive predators. A typical sequence is an initial fixation in the vicinity of the prey after the first movement followed by stationary waiting. Then when the prey moves again, the predator immediately strikes as the movement begins.

Line 220. The data has nothing to say about detection probability.

Line 221. However, the study did not cover a wide variety of motion speeds. Detection vs.

velocity may well be a complex function. There are many examples of animals that move extremely slowly and thereby seem to avoid stimulating motion detection vision.

Line 241. I am not comfortable with discussion of data that has been presented, or even briefly summarized in the results. Although it is in the supplementary data, since it has not been introduced even in a brief overview, for most readers the discussion is based on no information.

Summary: The paper would be more effective if it focused more clearly on the actual things that it explores. It is not a test of the role of motion on detection, and it should not claim that it is. It should recognize that effects of motion on precise localization is only one aspect of selection for motion crypsis. It should also recognize the a limited range of parameters have been tested. A more careful description and discussion of what is actually shown would make this a strong paper.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
RSPB-2019-1457

Smart et al present a study to investigate whether motion always breaks camouflage. Based on the premise that camouflaged animals need to move at certain times and are likely viewed in the visual periphery, the authors consider whether moving in a certain way helps to reduce the accuracy with which predators can pinpoint their new resting position. They also explored whether a flash manipulation aids in this objective. The results support the idea that fast movements over a short time period are most effective in this regard, and flash displays are mostly ineffective.

To the best of my knowledge, this study provides a novel examination of an under-appreciated facet of anti-predator behaviour and has done so in a clever way; achievable, in part, because the focal predators were humans and instructions could be clearly conveyed. I wonder just how well this approach could be implemented in other species, and at larger (and more appropriate for many species) scales? This paper does demonstrate the effect and will be a valuable contribution, but with this in mind, I would request that the authors address the choice of predator more explicitly. As we know, species differ in their sensory capabilities. The parameters set for the present study are necessarily chosen with human participants in mind, but they might not be applicable to many other species. For example, saccadic eye movements vary between species and as such the optimal duration of movement will likely vary. It is, of course, intriguing to consider the possibility that species would tailor their behaviour accordingly.

Although I found the topic, approach and overall message to be worthwhile, I would encourage the authors to consider the following comments:

• Mention earlier that the model predators are humans and that the approach is tailored to humans ("human participants" is mentioned in the abstract only). Include specifics on why particular durations/speeds of movement were used - expand on discussion of saccades at L55/56 and link this more clearly with parameters used in the study. What was the rationale for the different speeds? If there is no underlying basis for these, why not use a different set so that you didn't have to modify the pattern (doubling of speeds; although I get why 40 couldn't be used)?
• Although short, the results section is a little hard to get through as you work your way through the many different sub-tests. Could the statistical outcomes be presented in a table so that the reader can focus on words and outcomes separately?
• Greater attention on potential species differences (see above), future considerations (scaling up) etc. is required in the Discussion. Examination of response times (L241-6) could be removed to make room.

Additional minor comments:

L44 – it might be worth being more explicit in regard to motion dazzle to indicate that this is a result of the arrangement of static patterns which create a perceptual effect as the whole animal moves.
L83 – reference to '1/f function' is a little cryptic – I see from the reference that this is a matlab function but could be made clearer
L89 – I am not really clear on why the non-target screen turned plain grey. Why does it have to be unambiguous?

L118 – why were 162 trials used?

Decision letter (RSPB-2019-1457.R0)

09-Jul-2019

Dear Mr Smart:

We are writing to inform you that your manuscript RSPB-2019-1457 entitled "In the corner of the eye: camouflaging motion in the peripheral visual field" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be willing to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. We will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Proceedings B Office
mailto: proceedingsb@royalsociety.org

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Associate Editor, Comments to Author:

This study examines how motion in the visual periphery influences prey localisation. The role of peripheral vision in prey detection and localisation is an interesting question, with broad significance. However, the reviewers raise important concerns about what is being tested, the extent to which conclusions can be generalised to non-humans, and the relationship of the current findings to previous studies. Use of human subjects as predators has obvious advantages but the

ecological relevance needs to be clear, especially in terms of the motion parameters chosen, others not considered, and how these vary in importance/relevance between species (or between humans and other species). As highlighted by reviewer 1, the findings also need to be placed within the context of previous research on the role of motion parameters in object detection (mainly in humans). Reviewer 1 also points out that the experiment tests localisation rather than detection. This is important to evaluate the ecological relevance and significance of the experiments - do predators frequently localise prey in the visual periphery - or do they only detect prey peripherally then use the centre of the visual field for localisation? Also, it would be worth clarifying the hypothesised mechanism underlying the 'flash-display' treatment - and whether this is in fact the same as 'motion dazzle' or a 'startle display' (see reviewer 1's comments). The paper needs to be revised to address these issues before it can be considered for PRSLB - particularly in terms of evaluating the generality and importance of the findings.

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Reviewers' Comments to Author:

Referee: 1

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Summary: The paper would be more effective if it focused more clearly on the actual things that it explores. It is not a test of the role of motion on detection, and it should not claim that it is. It should recognize that effects of motion on precise localization is only one aspect of selection for motion crypsis. It should also recognize the a limited range of parameters have been tested. A more careful description and discussion of what is actually shown would make this a strong paper.

===

Referee: 2

RSPB-2019-1457

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To the best of my knowledge, this study provides a novel examination of an under-appreciated facet of anti-predator behaviour and has done so in a clever way; achievable, in part, because the focal predators were humans and instructions could be clearly conveyed. I wonder just how well this approach could be implemented in other species, and at larger (and more appropriate for many species) scales? This paper does demonstrate the effect and will be a valuable contribution, but with this in mind, I would request that the authors address the choice of predator more explicitly. As we know, species differ in their sensory capabilities. The parameters set for the present study are necessarily chosen with human participants in mind, but they might not be applicable to many other species. For example, saccadic eye movements vary between species and as such the optimal duration of movement will likely vary. It is, of course, intriguing to consider the possibility that species would tailor their behaviour accordingly.

Although I found the topic, approach and overall message to be worthwhile, I would encourage the authors to consider the following comments:

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• Although short, the results section is a little hard to get through as you work your way through the many different sub-tests. Could the statistical outcomes be presented in a table so that the reader can focus on words and outcomes separately?
• Greater attention on potential species differences (see above), future considerations (scaling up) etc. is required in the Discussion. Examination of response times (L241-6) could be removed to make room.

Additional minor comments:

L44 – it might be worth being more explicit in regard to motion dazzle to indicate that this is a result of the arrangement of static patterns which create a perceptual effect as the whole animal moves.
L83 – reference to '1/f function' is a little cryptic – I see from the reference that this is a matlab function but could be made clearer
L89 – I am not really clear on why the non-target screen turned plain grey. Why does it have to be unambiguous?
L118 – why were 162 trials used?

Author's Response to Decision Letter for (RSPB-2019-1457.R0)

See Appendix A.

RSPB-2019-2537.R0

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
Comments on authors' responses

I am satisfied with the responses to my initial queries.
• My suggestion to move statistical outcomes into a table would I agree create more difficulties and it certainly seemed easier to follow than during my initial read.
• I accept the suggestion that the results (qualitative) are likely broadly applicable across species, I think it is a little presumptive to assume this as a blanket rule given what we know about the perceptual and cognitive differences between species in a range of tasks. You could be specific about the qualitative outcomes you feel certain will hold and invite others to find otherwise.
• In agreement with reviewer 1, I think it unfortunate that latency data was restricted to the supplementary section; nevertheless, happy for this to be an editorial decision
• I understand now why there were 162 trials but the 3x3x3x3x2 design was not clear in the original submission. I still do not see where you state that all subjects received all conditions (3x3x3x3) on both screens.

Additional comments

• Please check the formatting of paragraphs in introduction
• I presume the third screen not gamma corrected.
• L83 – delete 'every'
• Methods - Do not believe it is mentioned that subjects received all conditions on both sides
• L 199 - Probably should define what you mean by 'first' and 'second order'
• Discussion – I agree that the data suggests it is possible to move but remain concealed. Of course, attention of the predator is now drawn to a smaller area so there is more to it than a one off event. For example, predators might then be able to use other mechanisms to locate prey or indeed otherwise adjust behaviour (to sit-and-wait). This was pointed out by reviewer 1 and perhaps could be a useful addition to the latter part of the discussion. For me it doesn't detract from your results, but sets up a premise for further investigations.

Review form: Reviewer 3

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
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No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Is it accessible?
N/A

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
In their manuscript the authors address a contemporary topic in the field of animal vision: the role of behaviour, here in terms of movement, as an additional component of the visual appearance of an animal to avoid detection/discrimination by an observer. By considering peripheral vision the authors have explored an extra component of the system which is not often considered in the animal vision literature.

My only suggestion to the authors is to remove the term 'colouration' from both the introduction (line 53) and abstract and replacing it by a more suitable term such as patterning which better reflect the stimuli used for their experiments. Once this has been done I would happily recommend the publication of the paper in Proceedings of the Royal Society B.

Decision letter (RSPB-2019-2537.R0)

21-Nov-2019

Dear Mr Smart:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

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In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

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Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Gary Carvalho
mailto: proceedingsb@royalsociety.org

Associate Editor Board Member
Comments to Author:
Both reviewers were satisfied that the revision addressed their original comments, and I agree that the key issues have been addressed, for the most part. The reviewers picked up a few additional minor errors to fix and I have a couple more below, and have one major remaining concern:

lines 252 - 255: One of the major issues for this kind of experiment is whether qualitative effects found for human subjects are likely to hold for other species, especially given how the study is framed. This was highlighted in the original reviews. You state here that 'qualitative effects should remain the same' for other species but provide no evidence for this claim. Why is that the case? Are there data that can support this claim? Are there data, for example, on saccadic latency

from other species? We do have some knowledge of acuity for other species in the central vs periperal visual field. How might this influence conclusions? This needs more discussion because it is critical to the argument that these experiments are relevant to predator-prey interactions. It's not sufficient to simply state that the qualitative results will hold for other species. An argument (with evidence) for why data from 'human predators' is likely generalisable to other species for this question should also be made in the introduction, which is currently very brief (so scope to expand). It should not be left to the last paragraph of the discussion.
minor comments:
line 33 - 34 - floating sentence - connect with subsequent paragraph
line 51: explain 'latency to saccade' in plain English at first mention for broad readership
line 142 - 143: please summarise results for response time in the main manuscript. Although the full statistical results are given in supplementary material, it is still necessary to say what they were in the results section, especially given that you discuss them in the discussion section.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
Comments on authors' responses

I am satisfied with the responses to my initial queries.
• My suggestion to move statistical outcomes into a table would I agree create more difficulties and it certainly seemed easier to follow than during my initial read.
• I accept the suggestion that the results (qualitative) are likely broadly applicable across species, I think it is a little presumptive to assume this as a blanket rule given what we know about the perceptual and cognitive differences between species in a range of tasks. You could be specific about the qualitative outcomes you feel certain will hold and invite others to find otherwise.
• In agreement with reviewer 1, I think it unfortunate that latency data was restricted to the supplementary section; nevertheless, happy for this to be an editorial decision
• I understand now why there were 162 trials but the 3x3x3x3x2 design was not clear in the original submission. I still do not see where you state that all subjects received all conditions (3x3x3x3) on both screens.

Additional comments

• Please check the formatting of paragraphs in introduction
• I presume the third screen not gamma corrected.
• L83 – delete 'every'
• Methods - Do not believe it is mentioned that subjects received all conditions on both sides
• L 199 - Probably should define what you mean by 'first' and 'second order'
• Discussion – I agree that the data suggests it is possible to move but remain concealed. Of course, attention of the predator is now drawn to a smaller area so there is more to it than a one off event. For example, predators might then be able to use other mechanisms to locate prey or indeed otherwise adjust behaviour (to sit-and-wait). This was pointed out by reviewer 1 and perhaps could be a useful addition to the latter part of the discussion. For me it doesn't detract from your results, but sets up a premise for further investigations.

Referee: 3

Comments to the Author(s).
In their manuscript the authors address a contemporary topic in the field of animal vision: the role of behaviour, here in terms of movement, as an additional component of the visual appearance of an animal to avoid detection/discrimination by an observer. By considering peripheral vision the authors have explored an extra component of the system which is not often considered in the animal vision literature.

My only suggestion to the authors is to remove the term 'colouration' from both the introduction (line 53) and abstract and replacing it by a more suitable term such as patterning which better reflect the stimuli used for their experiments. Once this has been done I would happily recommend the publication of the paper in Proceedings of the Royal Society B.

Author's Response to Decision Letter for (RSPB-2019-2537.R0)

See Appendix B.

Decision letter (RSPB-2019-2537.R1)

10-Dec-2019

Dear Mr Smart

I am pleased to inform you that your manuscript entitled "In the corner of the eye: camouflaging motion in the peripheral visual field" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Professor Gary Carvalho
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
Thank-you for carefully addressing the additional comments made by myself and two of the original reviewers. I think that the arguments provided for why the results from these experiments are likely applicable to other species (and therefore relevant for predator-prey interactions) are now convincing. The revised manuscript is more compelling and the broader significance is clearer. I am very happy to recommend its publication in Proc B.

Appendix A

Dear Editor,

Firstly, we would like to thank the referees for their comments. We have found them very helpful and, in addressing them, we think that the manuscript has been considerably improved.

Our responses (in ***bold italics***) to the comments (in plain text) are below. The line numbers refer to the modified manuscript.

Yours faithfully,

Ioan Smart, Innes Cuthill & Nick Scott-Samuel

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Associate Editor, Comments to Author:

This study examines how motion in the visual periphery influences prey localisation. The role of peripheral vision in prey detection and localisation is an interesting question, with broad significance. However, the reviewers raise important concerns about what is being tested, the extent to which conclusions can be generalised to non-humans, and the relationship of the current findings to previous studies. Use of human subjects as predators has obvious advantages but the ecological relevance needs to be clear, especially in terms of the motion parameters chosen, others not considered, and how these vary in importance/relevance between species (or between humans and other species). As highlighted by reviewer 1, the findings also need to be placed within the context of previous research on the role of motion parameters in object detection (mainly in humans). Reviewer 1 also points out that the experiment tests localisation rather than detection. This is important to evaluate the ecological relevance and significance of the experiments - do predators frequently localise prey in the visual periphery - or do they only detect prey peripherally then use the centre of the visual field for localisation? Also, it would be worth clarifying the hypothesised mechanism underlying the 'flash-display' treatment - and whether this is in fact the same as 'motion dazzle' or a 'startle display' (see reviewer 1's comments). The paper needs to be revised to address these issues before it can be considered for PRSLB - particularly in terms of evaluating the generality and importance of the findings.

The points raised about what is being tested, generalisation to non-humans and links to previous work are addressed below individually.

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Reviewers' Comments to Author:

Referee: 1

This is an interesting paper that describes a well-designed and executed experimental analysis of the effects of a small subset of visual motion parameters viewed in the visual periphery on subsequent fixation and localization of the moving stimulus. Human subjects gaze directly forward, and then observe a stimulus square moving briefly in their periphery (the object moves and disappears) and they are then challenged to click on the location where it was last seen. The pattern of the moving dot and its velocity and duration are varied, and localization accuracy is determined.

The experiment seems to be well carried out and analyzed and, for the most part, reasonable conclusions are drawn. A weakness of the paper is that it attempts to present this as an ecologically-relevant test of the processes underlying motion detection by visually hunting prey (or prey looking out for visually hunting predators). While there are some useful conclusions in this regard, the insights gained are not as useful or general as suggested.

As the authors indicate, in many predatory species, the spatial resolution of the visual periphery is many times lower than that of the center. The peripheral visual field is often served by motion-sensitive neurons with rather large receptive fields. Such neural circuits are extremely effective at detecting even very subtle motion (and often its direction), and they will often drive reflex shifts of the eye to place the moving image close to the center of the visual field. The moving object may then be detected by its shape (or color or pattern etc.) or, as is often the case with visual hunters that depend on motion, subsequent motion will reveal the precise location of the prey and elicit a strike. Given the relatively low acuity of the periphery, and large size of the receptive fields of the motion sensitive neurons, it does not seem that the system has evolved for precise localization of motion perceived in the periphery. Rather, there is two-stage process -- place the image somewhere in the higher acuity region of the retina, and then respond to subsequent motion (or spatial characteristics) when it occurs within this area of higher acuity. Thus a critical of role of the visual periphery is to detect whether, and roughly where, motion has occurred. Precise localization of the motion is probably not a critical first step.

We agree that when motion is directed in the periphery (as, we argue, will often be the case), the response is to orient towards the rough location and then search there or wait for further movement. We wanted to investigate the factors that determine exactly how (in)accurate that initial localisation is. If the target moves again, or is poorly camouflaged in the face of high-resolution vision, the answer would be rather trivial: immediate and accurate localisation. So, we wanted to determine localisation accuracy when the target, on stopping, is perfectly camouflaged.

This paper is presented as testing the effects of motion parameters on the analysis of detection and localization. However, in fact, there does not seem to be any test of how motion parameters impact detection: the viewers are required to attempt to localize the moving stimulus in every trial, so there is no test of detection. This limits the utility of the study, because it is not clear that precise localization of a moving target detected in the periphery is important in many predator-prey interactions.

If the authors could explain conditions (or provide examples) under which precise initial localization is critical, and if they refocus the manuscript on this process itself it would be considerably strengthened.

This is correct: our joint emphasis on both detection and localisation was misplaced, and we have changed the manuscript to remove references to detection. The thrust of our argument now centres around localisation.

I would also point out that there is a body of literature on the role of motion parameters and surface parameters (e.g. luminance contrast, pattern contrast, chromatic contrast) on detection of moving objects. It is well-established, for example that most motion perception relies on luminance contrast, so this result is interesting, but not novel. It would be worth reviewing some of this literature because some of the conclusions reached in this paper are at odds with these earlier studies. For example, short duration, middle amplitude, high velocity, abrupt movements have been shown to be optimally effective at eliciting visual attention. This seems to contradict the results here. Part of the issue may well lie in differences in the experimental task (e.g. localization versus

initial detection), and in details such as the range of amplitudes considered, and whether or not the moving target remains visible or disappears.

This is perfectly correct and, were we to be investigating initial detection of a moving target, would be highly relevant. However, in light of our new focus (localisation), discussing this literature would detract from this.

Specific comments:

Line 9. This is true of some predators but not all.

Good point. Addressed (line 8-9).

Line 13-14. "The same logic applies…". I'm not sure I agree with this. Precise location and detection are not identical problems. A neural circuit with a large receptive field can be superb for detection of motion, but not so good for localization. These really are two distinct processes.

Good point. Addressed (lines 13-14).

Line 23-24. It is unclear what is meant by this statement. Are you referring to a non-moving target?

Clarified (line 24).

Line 25. This is true in some, but not all, animal species.

Good point. Clarified (line 25).

Line 40. This is true, although there are animals such as stick insects, chameleons and vine snakes that use plant-like motion as a form of camouflage.

Good point. Clarified (line 41) by adding the following reference: Cuthill I.C., Matchette S.R., Scott-Samuel N.E. 2019 Camouflage in a dynamic world. Current Opinion in Behavioral Sciences 30, 109-115..

Line 44. What you refer to as "motion dazzle" is not really tested in this experiment. "Motion dazzle" refers to the example where an animal flashes a shiny surface that startles or overwhelms the predator's visual system. There is no way that the stimulus described in this experiment would have this effect on the subjects. The experiments described in this paper test something closer to the "flash concealment hypothesis" (see Hasson 1991 Trends Ecol. Evol.,6, 325–329).

Hasson's TREE article centres on pursuit-deterrence signals rather than disruption of an attack that has been launched, so we feel the better reference is to Hailman's (1977, p.182) discussion of 'startle deception'. What we didn't make clear in the manuscript was that we are talking about something rather different, because 'startle deception' and 'dazzle' are thought of as effects on a predator that has fixated on the target and is about to strike. We are talking about a putative 'anchoring' effect in peripheral vision. We have clarified this and reference to motion dazzle (originally lines 42+) has been removed.

Line 58. Duration and speed are not the only key parameters of transient motion, and they may not be the most important. I'm not suggesting it is invalid to examine these parameters, but it is

misleading to suggest that they are the only important factors. In theoretical (and experimental studies) of motion detection, amplitude of motion across the retina has also proven to be very important. It is, of course, awkward to include this in the analysis because it co-varies with the other two parameters. Never-the-less, motion detection circuits tend to be tuned to respond optimally to certain motion amplitudes. Obviously minimum resolution is a critical parameter for motion detection, so amplitude cannot simply be ignored. Further, abruptness of movement (possibly even acceleration) has been shown to be a critical parameter.

True. We note that duration and speed are not the only key parameters, and that these are just the ones we concentrate on here (line 52).

Line 59. It does not seem to me that the stimulus employed here represents a startle display. The second idea – what I have called "flash-concealment" above – is closer to what is being tested. This is not like the abrupt flash of a moth or butterfly wings, but more similar to tail-wagging or head-bob displays given by some lizards right before they move quickly into hiding.

Correct (see above) - now clarified (line 56 and line 58).

Line 68. It is not clear to me how detection is tested in this experiment.

Correct. Reference to detection removed (line 63).

Line 107. This stimulus does not, to me, seem to represent the definition of a deimatic display. I doubt it has any startle or distraction effect on the viewer. As I suggest above, I think it fits better with the idea of a "flash-conealment" type display. Rather than interfere with the function of the nervous system, it is hypothesized to elicit a strong attention response that interferes with the ability to track the motion that follows immediately after it. "Deimatic" is a rather obscure term that most will be unfamiliar with (I had to look it up), and it does not apply particularly well in this case.

You are right that our stimulus is not what people are thinking of in terms of Hailman's startle-deception or a deimatic display – see above. We only used the term 'deimatic' because it has made a comeback, with a raft of new papers discussing how this defence may or may not work (e.g. Holmes, G.G., Delferriere, E., Rowe, C., Troscianko, J. & Skelhorn, J. 2018 Testing the feasibility of the startle-first route to deimatism. Sci. Rep. 8; Skelhorn, J., Holmes, G.G. & Rowe, C. 2016 Deimatic or aposematic? Anim. Behav. 113, E1-E3; Umbers, K.D.L., Lehtonen, J. & Mappes, J. 2015 Deimatic displays. Curr. Biol. 25, R58-R59; Umbers, K.D.L. & Mappes, J. 2016 Towards a tractable working hypothesis for deimatic displays. Anim. Behav. 113, E5-E7). However, the sense is perfectly clear without 'deimatic', so we have removed it. The section now reads (lines 56 – 58) "These are usually considered to be displays that startle a predator or interfere with identification [14-17] when the predator has already fixated the prey and is initiating an attack. Here, we explore a different possible advantage that occurs when prey movement occurs in peripheral vision…". Furthermore, the term 'deimatic' throughout the manuscript has been removed and replaced with 'startle'.

Commented [I1]: I realise that even though we may have clarified L56-58 the term was used throughout (in a sensible enough way). However, to prevent any difficulties I have replaced deimatic with startle.

Lines 110-127. I do not see where "detection" is tested in this methodology. In every case the subject is ultimately "informed" of which side the motion occurred, and then tries to locate it. Where is the ability to detect, or not detect the stimulus tested?

Correct. Reference to detection removed (line 109).

Line 143. What is the "central screen?" This was not mentioned in the methods.

Now clarified (lines 71-72): there were three screens, a central one for fixation and two peripheral ones for stimulus presentation. It now reads "The screens were positioned so that the centre of each one was 50 cm from the subject and at an angle of 65° from a fixation cross on a third, central screen."

Line 145. If "response time" results are not presented in the main body of the paper, it should not really be raised in the discussion.

Perhaps this is an editorial decision? (See also comments on lines 194-195, 241.) Supplementary material is currently presented alongside the paper, and forms part of the story we wish to tell. It is not essential to the point we are making (hence supplementary) but it supports the argument in a useful way. Furthermore, it would be as accessible as the main article, both being downloadable from the same location on the journal website. We submit that it is therefore appropriate to refer to this material in the discussion of our results.

Line 190. I do not see how these experiments lead to any conclusions about "detecton." Only localization has been tested. This is not a trivial point, as I discuss later.

Correct. Reference to detection removed (line 187).

Line 191 – discuss this conclusion with reference to other work, the role of the visual periphery in motion detection and the ecological relevance of the work.

The referee would like some specific citations, but none are given and we are unsure exactly what work is meant. Are they able to offer some guidance? Note that further references on detection itself would only be indirectly relevant, given the clarified focus on localisation.

Line 192 – the conclusion that a luminance matched target is more difficult for motion perception is very well established.

True. References to relative weakness of second-order motion stimuli inserted (lines 188-190): "This latter criterion would push the stimulus towards being second-order, and it is well known that such stimuli are far weaker than their first-order counterparts [e.g. 37, 38]."

Line 194-195. It is not really useful to discuss response times or directional errors in the discussion since no results concerning response times are included in the "results section" of the paper.

Supplementary material is as accessible as the main text and it seems common practice, these days, to refer to it in papers: see also the responses to the comments on lines 145, 241.

Lines 205-208. I'm skeptical about this conclusion. Motion sensitive predators will tend to fixate in the approximate area of the initial motion, then wait for the next movement to occur, at which point they can fixate much more effectively because the higher resolution portion of the visual field is likely to cover the location of the prey. Unless an animal waits until the predator shifts its gaze again, intermittent movement will not be of much help. In fact I have observed a number of predation events involving highly motion sensitive predators. A typical sequence is an initial fixation in the vicinity of the prey after the first movement followed by stationary waiting. Then when the prey moves again, the predator immediately strikes as the movement begins.

This is interesting, and it would be a fruitful area for future research, because we know of no published work that analyses the fine details of both predator and prey in this manner. So, scepticism is healthy, but not a reason to reject our proposition!

Line 220. The data has nothing to say about detection probability.

True. Reference to detection removed (line 220).

Line 221. However, the study did not cover a wide variety of motion speeds. Detection vs. velocity may well be a complex function. There are many examples of animals that move extremely slowly and thereby seem to avoid stimulating motion detection vision.

A more comprehensive coverage of each parameter would certainly be of interest. The range of motion speeds was designed to bracket saccadic latency for our human observers; thus, we have three levels, one below, one above, and one approximating the time required for a single saccade. Furthermore, we wanted to examine the effects of speed (slow, medium, fast) and surface patterning. As a result, we had a multi-factor design and extending the number of levels in any of the parameters would have created a factorial increase in the number of treatment combinations. We feel that our initial range (in an already multi-factor design) was a sensible starting point.

Line 241. I am not comfortable with discussion of data that has been presented, or even briefly summarized in the results. Although it is in the supplementary data, since it has not been introduced even in a brief overview, for most readers the discussion is based on no information.

See our response to comments on lines 145, 194-195. We would be guided by the editor as to journal policy on this matter.

Summary: The paper would be more effective if it focused more clearly on the actual things that it explores. It is not a test of the role of motion on detection, and it should not claim that it is. It should recognize that effects of motion on precise localization is only one aspect of selection for motion crypsis. It should also recognize the a limited range of parameters have been tested. A more careful description and discussion of what is actually shown would make this a strong paper.

We hope that we have refocussed the manuscript as the reviewer wishes by addressing their comments.

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Referee: 2

RSPB-2019-1457

Smart et al present a study to investigate whether motion always breaks camouflage. Based on the premise that camouflaged animals need to move at certain times and are likely viewed in the visual periphery, the authors consider whether moving in a certain way helps to reduce the accuracy with which predators can pinpoint their new resting position. They also explored whether a flash manipulation aids in this objective. The results support the idea that fast movements over a short time period are most effective in this regard, and flash displays are mostly ineffective.

To the best of my knowledge, this study provides a novel examination of an under-appreciated facet of anti-predator behaviour and has done so in a clever way; achievable, in part, because the focal predators were humans and instructions could be clearly conveyed. I wonder just how well this approach could be implemented in other species, and at larger (and more appropriate for many species) scales? This paper does demonstrate the effect and will be a valuable contribution, but with this in mind, I would request that the authors address the choice of predator more explicitly. As we know, species differ in their sensory capabilities. The parameters set for the present study are necessarily chosen with human participants in mind, but they might not be applicable to many other species. For example, saccadic eye movements vary between species and as such the optimal duration of movement will likely vary. It is, of course, intriguing to consider the possibility that species would tailor their behaviour accordingly.

We would argue that although there are almost certainly quantitative differences across species, the qualitative effects should remain the same. So, while the exact figures for human observers will no doubt differ from other species, the pattern of results should hold generally. It would be very difficult to carry out similar experiments with non-human subjects; we chose humans because it allowed us to be very specific in what we required our observers to do, and what we measured.

Although I found the topic, approach and overall message to be worthwhile, I would encourage the authors to consider the following comments:

• Mention earlier that the model predators are humans and that the approach is tailored to humans ("human participants" is mentioned in the abstract only). Include specifics on why particular durations/speeds of movement were used - expand on discussion of saccades at L55/56 and link this more clearly with parameters used in the study. What was the rationale for the different speeds? If there is no underlying basis for these, why not use a different set so that you didn't have to modify the pattern (doubling of speeds; although I get why 40 couldn't be used)?

Reference to humans inserted (line 43). Justification for the range of values for the speed and duration parameters has been added (lines 96 - 99): "Duration of movement (duration) had three levels that were designed to bracket saccadic latency for our human observers [32]: 100, 200 & 400 ms. Speed had three levels that were designed to provide a range of velocities (relatively slower and relatively faster) around data on movement speeds of Zootoca vivipara [see 33]: 10, 20 and 35 deg/s." See also the response to the comments on line 221 by referee 1.

• Although short, the results section is a little hard to get through as you work your way through the many different sub-tests. Could the statistical outcomes be presented in a table so that the reader can focus on words and outcomes separately?

We did consider this, but the very complexity of the design means that the reader has to be talked through such a table line by line and so, in the end, combining words and stats in the main text is a more compact way of doing this and saves the reader switching to and from a table.

• Greater attention on potential species differences (see above), future considerations (scaling up) etc. is required in the Discussion. Examination of response times (L241-6) could be removed to make room.

See our response to the comment on species differences above. This argument has also been added to the manuscript to address species differences (lines 252-258): "Whilst there are almost certainly quantitative differences across species, the qualitative effects should remain the same. So, while the exact figures for human observers will no doubt differ from other species, the pattern

of results should hold generally. Furthermore, it would be very difficult to carry out similar experiments with non-human subjects; we chose humans because it allowed us to be very specific in what we required our observers to do, and what we measured." Additionally, we feel that discussion on response time supports our argument; see our response to the first reviewers' comments on lines 145, 194-195, 241.

Additional minor comments:

L44 – it might be worth being more explicit in regard to motion dazzle to indicate that this is a result of the arrangement of static patterns which create a perceptual effect as the whole animal moves.

The references to motion dazzle are, we think, a distraction from the type of effect we tested here, and so have been removed (see reviewer 1's comment on line 44, above).

L83 – reference to '1/f function' is a little cryptic – I see from the reference that this is a matlab function but could be made clearer

Yes, this was rather nerdy. Now clarified (lines 77-81): "Within each trial the target would move on a background generated by a 1/f function [30], representing a generic textured background to which visual systems are hypothesised to be adapted [31]. Spectral analysis of natural scenes shows that amplitude is inversely related to spatial frequency, f; hence the 1/f function [31]."

L89 – I am not really clear on why the non-target screen turned plain grey. Why does it have to be unambiguous?

That our focus was on localisation, rather than detection, has now been clarified throughout the manuscript (see response to reviewer 1 comments). If participants who had maybe not detected the target at all could guess at a location on any one of three screens, then the analysis of click-to-target error would be problematic. Therefore, we reduced the decision to, essentially, "it's here somewhere, but where exactly do you think it is?"

L118 – why were 162 trials used?

This is because there were three patterns, three durations, three speeds, three flash conditions and two sides that the stimulus could appear, giving a 3x3x3x3x2 design when every possible combination appeared once for each participant.

Appendix B

Dear Professor Carvalho,

We would like to thank you for inviting us to resubmit and, also, we would like to thank the referees for their comments. We have found them insightful, and helpful.

Our responses (in ***bold italics***) to the comments (in plain text) are below. The line numbers refer to the modified manuscript.

Yours faithfully,

Ioan Smart, Innes Cuthill & Nick Scott-Samuel

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Associate Editor Board Member

Both reviewers were satisfied that the revision addressed their original comments, and I agree that the key issues have been addressed, for the most part. The reviewers picked up a few additional minor errors to fix and I have a couple more below, and have one major remaining concern:

lines 252 - 255: One of the major issues for this kind of experiment is whether qualitative effects found for human subjects are likely to hold for other species, especially given how the study is framed. This was highlighted in the original reviews. You state here that 'qualitative effects should remain the same' for other species but provide no evidence for this claim. Why is that the case? Are there data that can support this claim? Are there data, for example, on saccadic latency from other species? We do have some knowledge of acuity for other species in the central vs periperal visual field. How might this influence conclusions? This needs more discussion because it is critical to the argument that these experiments are relevant to predator-prey interactions. It's not sufficient to simply state that the qualitative results will hold for other species. An argument (with evidence) for why data from 'human predators' is likely generalisable to other species for this question should also be made in the introduction, which is currently very brief (so scope to expand). It should not be left to the last paragraph of the discussion.
minor comments:

We agree that we had not formally addressed the generalisations and inferences that could be made from 'human predators'. To amend this, we discuss three phenomena that, generally, hold true across species. Firstly, we highlight that many species have a region of their visual field that has a higher concentration of cone photoreceptors (an area centralis) that corresponds to a high-resolution region, and that this diminishes with increasing eccentricity. So, "peripheral vision" is a widespread phenomenon (although some fish have a fairly even photoreceptor density). Secondly, we highlight the ubiquity of fixate-saccade strategies across taxa, relying on Mike Land's recent review (and lifetime's work). Finally, we remind the reader that no information is gained whilst saccading. Considering these three points, a viewer is likely to redirect its gaze, via saccades, at which moment the viewer is effectively blind, toward a peripheral target so that it can direct the higher acuity region of the visual field toward the target and better localise it. We hope that this information addresses the similarities in the visual systems of humans and other animals, and suggest that it is plausible that the results from 'human predators' apply to other animals, albeit with differences in detail as to where the areas of reduced acuity are in the visual field, and rapidity of saccade (e.g. with a rapid eye movement, or slower head/body orientation). These points have been interweaved through the manuscript; see their additions below:

L67 – 74: "Many species use saccades alongside fixations to perceive their environment; typically, these are eye-saccades but can also be head-saccades, in the case of birds, or body-saccades, in the case of insects [14]. Furthermore, many species have a region of the visual field that has a high concentration of cone photoreceptors (e.g. area centralis) [see 14, 15; table 3 pg. 187], giving good visual acuity; as eccentricity from this region increases photoreceptor density, and thus acuity, decreases. Amongst other things, the fixate-saccade strategy allows an organism to divert the higher-resolution region of its visual field toward an object [14]."

L222 – 225: "Considering that the fixate-saccade strategy is ubiquitous, this suggests that the prevalence of the intermittent motion observed in many animals [35, 47-54], which is often attributed to the benefits of image stabilisation for the prey species itself [35, 52, 53, 55], could instead (or additionally) serve to reduce a predator's ability to localise a prey [35, 52]."

L276 – 289: "Whilst there are almost certainly quantitative differences across species, the qualitative effects should remain the same. If we consider the ubiquity of the fixate-saccade strategy [14], and the distribution of photoreceptors that results in a high-resolution region surrounded by an area where resolution drops with increasing eccentricity, we could expect these results to occur in many other species. So, while the speed and mechanism (eye, head or body movement) will no doubt differ between humans and other species, the pattern of results should hold generally. In particular, because limited information is acquired during a viewer's gaze shift, to reduce the probability of being located accurately an animal should move and stop before it can be fixated, and limit the amount of visual information available while moving with coloration that approximates the mean luminance of the background and lacks patterning. It would be very difficult to carry out similar experiments with non-human subjects; we chose humans because it allowed us to be very specific in what we required our observers to do, and what we measured."

line 33 - 34 - floating sentence - connect with subsequent paragraph

The floating sentence (L48 - 49) has been joined to the subsequent paragraph

line 51: explain 'latency to saccade' in plain English at first mention for broad readership

Fair comment, L64 – 67 now reads "Studies on humans suggest that the perceived position of a moving target is predicted via motion extrapolation, and that localisation is affected by the time it takes for the observer to move their eyes toward the target (i.e. the saccadic latency) [13]."

line 142 - 143: please summarise results for response time in the main manuscript. Although the full statistical results are given in supplementary material, it is still necessary to say what they were in the results section, especially given that you discuss them in the discussion section.

The MS now indicates that the supplementary supplies a "… detailed analysis of response time…" (L159 – 160). Additionally, a summary paragraph has been added (L192 – 198), which reads: "Modelling for response time indicated a significant interaction between pattern and flash when the stimulus moved for 100 ms, with pattern only having a significant effect in the no flash condition (Supplementary Material). Specifically, mean luminance had longer response times than background matching or black patterning, which did not differ. At 200 ms there was a significant effect of flash, with the no flash condition having a longer response time than the flash conditions. At 400 ms there was a significant effect of speed, where an increase in speed increased the response time."

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Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
Comments on authors' responses

I am satisfied with the responses to my initial queries.

- My suggestion to move statistical outcomes into a table would I agree create more difficulties and it certainly seemed easier to follow than during my initial read.

- I accept the suggestion that the results (qualitative) are likely broadly applicable across species, I think it is a little presumptive to assume this as a blanket rule given what we know about the perceptual and cognitive differences between species in a range of tasks. You could be specific about the qualitative outcomes you feel certain will hold and invite others to find otherwise.

We agree that the statement requires additional information to strengthen its claim. Please see the response to the editor's comments.

- In agreement with reviewer 1, I think it unfortunate that latency data was restricted to the supplementary section; nevertheless, happy for this to be an editorial decision

Please see response to the editor's comments on Line 142 - 143

- I understand now why there were 162 trials but the 3x3x3x3x2 design was not clear in the original submission. I still do not see where you state that all subjects received all conditions (3x3x3x3) on both screens.

We have now clarified that each participant received all conditions (L131 – 133). "Each participant completed six practice trials followed by 162 test trials, which were broken into three blocks of 54. Therefore, participants received all conditions (3 x 3 x 3 x 3) on both screens."

Additional comments

- Please check the formatting of paragraphs in introduction

We have checked the formatting, and following comments from the editor have joined the floating sentence to the succeeding paragraph.

- I presume the third screen not gamma corrected.

Correct. Clarified (L93 – 95): "The screens were positioned so that the centre of each one was 50 cm from the subject and at an angle of 65° from a fixation cross on a third, not gamma corrected, central screen."

- L83 – delete 'every'

Deleted. (L98)

- Methods - Do not believe it is mentioned that subjects received all conditions on both sides

Please see the response to the comment above.

- L 199 - Probably should define what you mean by 'first' and 'second order'

We have expanded the section to make this clear. L203 – 208: "A first-order stimulus is defined by intensity differences between target and background, while a second-order stimulus is defined by a difference in some other property, (e.g. contrast or pattern). Matching the mean luminance of the target and background pushes the stimulus towards being second-order, and is well known that such stimuli are far weaker than their first-order counterparts [e.g. 39, 40]."

- Discussion – I agree that the data suggests it is possible to move but remain concealed. Of course, attention of the predator is now drawn to a smaller area so there is more to it than a one off event. For example, predators might then be able to use other mechanisms to locate prey or indeed otherwise adjust behaviour (to sit-and-wait). This was pointed out by reviewer 1 and perhaps could be a useful addition to the latter part of the discussion. For me it doesn't detract from your results, but sets up a premise for further investigations.

We agree that our examination only considered one bout of movement, and the suggestion that 'predators may sit-and-wait for subsequent movement' and some additional things that are worth considering have been introduced:

L268 – 275: **"It is feasible that predator attention is drawn to the first instance of movement and, subsequently, predators could sit-and-wait for additional movement. However, this presupposes that the predator was able to recognise the source of movement as potential prey, which may not be the case. Additionally, it may not be beneficial for the predator to sit-and-wait for subsequent movement from an uncertain source; continuing to actively search the environment may be more beneficial. Furthermore, we must consider how noisy environments can be (e.g. foliage in the wind) and the impact that this may have upon localisation of a moving target [8]."**

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Referee: 3

Comments to the Author(s).
In their manuscript the authors address a contemporary topic in the field of animal vision: the role of behaviour, here in terms of movement, as an additional component of the visual appearance of an animal to avoid detection/discrimination by an observer. By considering peripheral vision the authors have explored an extra component of the system which is not often considered in the animal vision literature.

My only suggestion to the authors is to remove the term 'colouration' from both the introduction (line 53) and abstract and replacing it by a more suitable term such as patterning which better reflect the stimuli used for their experiments. Once this has been done I would happily recommend the publication of the paper in Proceedings of the Royal Society B.

This is a fair comment. The word 'colouration' has been removed from the introduction (L 76) and the abstract, and has been replaced with the word 'pattern'.