

## Peer Review Overview

**Manuscript Title:** The role of temporal cortex in the control of attention

Received	Nov 27,2021
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### 1st Decision letter

**Reference:** CRNEUR-D-21-00068

**Title:** The role of temporal cortex in the control of attention

**Journal:** Current Research in Neurobiology

Dear Dr. Ramezanpour,

Thank you for submitting your manuscript to Current Research in Neurobiology.

The reviewers recommend reconsideration of your manuscript following major revision. I invite you to resubmit your manuscript after addressing the comments below. Please resubmit your revised manuscript by Mar 01, 2022.

When revising your manuscript, please consider all issues mentioned in the reviewers' comments carefully: please outline in a cover letter every change made in response to their comments and provide suitable rebuttals for any comments not addressed. Please note that your revised submission may need to be re-reviewed.

Current Research in Neurobiology values your contribution and I look forward to receiving your revised manuscript.

*CRNEUR* aims to be a unique, community-led journal, as highlighted in the [Editorial Introduction](#). As part of this vision, we will be regularly seeking input from the scientific community. We encourage you and your co-authors to take the [survey](#) as part of the editorial.

Kind regards,

Christopher I. Petkov  
Editor in Chief  
Current Research in Neurobiology

## Comments from Editors and Reviewers:

### Reviewer #1:

#### General comments

This article provides a sweeping review of recent experiments about the importance of temporal visual cortex in the control of visual attention. The main emphasis is on how recent fMRI and recording experiments in nonhuman primates have provided new evidence that these areas are part of a "temporal attention network" that is not just the recipient of attention control signals but that also plays an important role in coordinating attention with task-related cognitive processes. The tone and treatment of the material is reasonably fair and balanced (although there is a bit of extra emphasis on the "selective tuning" model by John Tsotsos and colleagues), and the authors do a good job of citing older work and putting the new findings into an appropriate historical context.

There are a few points that piqued my interest in particular, or that I thought might benefit from some additional explanation, and those are outlined in the major comments below.

To indicate page numbers, I will refer to the pages in the merged pdf document provided for review (i.e., highlights on page 4).

#### Major comments

On page 16, you make the point that there is evidence that a TAN exists in both monkeys and humans, based on the observation that similar tasks are able to localize brain regions using fMRI in both species. Is it clear that these regions are indeed homologous, based on other factors (e.g., connectivity, deficits when damaged)? Playing devil's advocate, one might expect that some brain region(s) should be preferentially activated in the ventral stream during these tasks, but that this might occur for very different reasons in monkeys vs. humans (for example, if they used different strategies). If that were the case, then they might not actually be functional homologues. Are there additional reasons for judging these to be homologues, rather than something less conserved?

On page 17, you make the interesting comment that the location of these TAN regions might be somehow dictated by the adjacent feature/priority maps, and the mechanistic need for lateralized local connectivity in order for the TAN to accomplish its particular function. There are two points I wonder if you might comment on. First, does this speak to supra-modal attention, and the placement of these regions near other sensory cortices (esp auditory) in addition to being near visual feature maps? Second, does this provide any insight into the different location of the TAN in humans vs. monkeys? Is the TAN in humans surrounded by cortical areas that are needed for some attention capacities that are not present in monkeys? A related point comes up at the end of the article (page 22) when you discuss possible ecological benefits.

On page 19, you make the point about the distinct topography of the TAN and how that would provide surround inhibition. How would this work with objects that are very elongated? This may seem picky, but elongated objects are often very relevant to primates. For example, when leaping through the forest, I might select a branch to grab based on how that particular branch is connected to the trunk of a particular tree. How do you envision that this type of selection takes place?

Throughout the article, the experimental findings are placed in a broader theoretical context by

references to the 'selective tuning model of attention'. This was ok, but not entirely satisfactory. It is unclear whether you consider the other theories of attention mentioned earlier in the article to be incompatible with the experimental findings, or simply irrelevant (e.g., because their features do not map onto these data). Some additional framing and justification for the focus on this particular model would be helpful. On a related point, does the selective tuning model make any specific predictions that can now be tested? Does the TAN have functional properties that you would only expect if some distinguishing properties of the model were correct? There are some comments along these lines, but they are stated more in terms of findings being 'consistent with' the model, and these consistent observations might be true for a broader range of models and not just the selective tuning model. Please clarify these points.

Minor comments

Page 10. Typo: Rohtblat

Page 13, top paragraph. The description of the experimental paradigm here was hard to follow. Perhaps a diagram would help clarify, if you think it is worth it.

Page 13, middle. Has "SC" been defined somewhere?

Page 14, toward the bottom. This is a very long paragraph and I wonder if it would be better to start a new paragraph when you start discussing "Another common denominator". On that point, not all of the studies referenced involve planning saccades, so it is not clear that this point is indeed common to all of the studies.

Page 14, last line. Not sure what you mean by "modulatory quantity being attention"

Page 15, first line. Again, not so sure what you mean here. What is the coordinate system for attention-centered, as opposed to eye-centered?

Page 16. "hired"? Perhaps: "now using the same behavioral paradigms as in monkey studies..."

Page 16, about  $\frac{3}{4}$  the way down. Typo: "findings"

Page 17, First question "what is the relationship between feature selectivity..." I do not fully understand what you mean by this, or why the answer would be important. Please clarify.

Page 20, 9 lines from bottom. Typo: "supports"

Page 20, 8 lines from bottom. "white" matter?

Page 21, top. You don't say much about connectivity of mid-STS. Are there also inputs from pulvinar and superior colliculus?

## Reviewer #2:

### General comment:

1) In this review paper, the authors discuss the idea of a Temporal Attention Network (TAN), consisting of the posterior dorsal inferior temporal cortex (pITd), the gaze following patch (GFP), and the mid-superior temporal sulcus (mid-STs). Evidence is presented from non-human primates (NHPs) that these brain regions respond to attentional demands, are connected with the dorsal and ventral attention networks, as well as various visual areas, and are implicated in social behavior. Overall, the idea of a TAN is well argued and timely considering recent NHP studies. However, while it is useful to incorporate theoretical/computational models of attention, the reader would be better served by a more equitable coverage of existing models, rather than focusing on models from one lab. Further, Figure 1 could be reworked to enhance the narrative; and the social interactions section could be better substantiated with more published work. Specific comments to accordingly help with revisions below.

### Specific comments:

2) RE: Visual attention section, 4th paragraph: "In addition to the premotor theory of attention, several other theories such as biased competition [4,33], selective tuning [34,35], and the rhythmic theory of attention [36]...Nevertheless, here we briefly review the concept of the selective tuning model [37] which is relevant for temporal cortex participation in attentional control." As the authors point out, there are a number of theories of attention, e.g., Reynolds and Heeger (2009, Neuron), Itti and Koch (2001, Nat Rev Neurosci), Olshausen et al. (1993, J Neurosci), Bundesen et al. (2005, Psychol Rev) in addition to those mentioned. A number of these theories are "relevant for temporal cortex participation in attentional control". Rather than only focusing on the selective tuning model, it would be more useful to the reader to rework this paragraph, and the rest of the review, to better reflect the other contributions as well. One possibility is to rephrase such that the multiple levels, "winner take all" mechanisms, etc, are common aspects of multiple models.

3) RE: Temporal cortex participates in attentional control section, Figure 1. To me, Figure 1 does not significantly enhance understanding of early vs late attentional selection beyond what is in the text. Instead, it may be more useful to either show data from the discussed paper by Roitblat and Pribram or other relevant studies, or provide a toy example of what the neural responses themselves look like during early and late selection (e.g., the time courses of neural activity surrounding the stimulus and response).

4) RE: "Cognitive programs". The hypothesis of "cognitive programs" as proposed by Tsotsos and Kruijne (2014, Frontiers) is a useful approach to understanding executive functions and the control of visual attention. However, there are other relevant frameworks here, e.g., Bundesen et al. (2005, Psychol Rev), Miller and Buschman (2013, Curr Opin in Neurobiol), Botvinick et al. (2009, Cognition), etc. It would be more useful to the reader to rework the text covering "cognitive programs" to better reflect other relevant contributions to cognitive control as well.

5) RE: the section "What do the TAN regions have in common". This section presumes that the IT cortex is involved in both attentional processes and broader executive functioning. However, the fact that behavioral tasks used have an executive component does not necessarily mean the TAN is involved in executive functioning itself. Likewise, while the disruption of prefrontal cortical activity from IT cooling suggests the region is involved in attentional processing, it does not imply the disruption is due to

disrupting "cognitive programs" as described in the text. Please elaborate with more evidence that "the neural circuits in the TAN are not just passive receivers of attention signals, but they also significantly contribute to executive control of visual attention and implementation of cognitive programs during complex behaviors." Otherwise, it might be more appropriate to better balance the hypotheses about the TAN with the contributions of prefrontal and parietal cortex to executive functioning. This also applies to the conclusions section of the paper.

6) When describing the human correlates of the TAN in fMRI studies (page 12 on my copy), the authors mention the areas are clearly far from the TPJ but do not describe the areas of the human TAN in detail. Please describe or show the locations of the human TAN.

7) RE: the section "Implications of active vision in temporal cortex for social interactions" is reliant on "anecdotal reports of the neurons in the STS representing others' actions [181]". It also relies on unreferenced assumptions of parsimony and ecological benefit about social cues and representations in the temporal cortex. Currently, this seems quite speculative. I might suggest providing additional evidence of social-related activity in the temporal cortex. For example, single- and multi-unit recordings in humans have reported mirror neurons and other neurons related to action perception in temporal cortex (Mukamel et al., 2010, *Current Biology*). Further, a number of other brain areas have been shown to constitute social neural networks, e.g., premotor and posterior parietal cortex (Rizzolatti and Sinigaglia, 2010), orbitofrontal cortex (Azzi et al., 2012), anterior cingulate cortex (Chang et al., 2013; Yoshida et al., 2012; Haroush and Williams, 2015), etc. How would the TAN relate to these other areas? Additionally, similar to point 5 above, why is it necessary that these computations take place in the TAN and not in other areas of the frontal and parietal lobes?

Minor comment:

8) From the main text: "Since the GFP is very close to the pITd, one might expect that their connections should not be drastically different than the pITd." Possibly, but not necessarily so, e.g., dorsal and ventral LIP have distinct connectivity patterns. Perhaps rephrase the quoted sentence.

### **Reviewer #3:**

This review article summarized the literature on the possible involvement of the temporal cortex in control of attention. This is a timely opinion because traditionally the temporal cortex has been considered as the center for passive object recognition, however recently accumulating evidence supports that the temporal cortex is also actively involved in control of object-based attention. In general, the manuscript comprehensively summarizes the current status of the field, but I also have to raise several issues, which are unclear and the authors have to reconsider.

Figures 1 and 2 do not well match the descriptions in the text. I recommend the authors to reconsider the relationship between Figure 1 and the text. Figure 1 is explained in the initial half of the 2nd paragraph of page 6. However, the text (especially, the part "They showed initially the neural responses ..... filtering via the IT cortex [119] (see Figure 1)") does not seem to follow the content of the figure. I recommend to revise the text, or the content of Figure 1. As for Figure 2, there are many names of brain areas (such as MTC, STG, STS, IT, pIT, cIT, aIT, VPA, GFP...) and pathway (such as TAN), however to many of the readers, their anatomical locations are not obvious. Therefore, I recommend the authors to use a figure which explains the anatomical locations and functions of the areas described in the text. In this aspect, the authors' intention of Figure 2 is not clear to me. Intention of 2 right black panels at the

bottom is not clear to me. Thus, I think Figure 2 needs to be revised to give sufficient information described in the text to the readers.

The authors need to be careful about font usage. The texts are bold in some cases or written in different fonts.

Typos (?);

The first line of 2nd paragraph of page 4; "superior temporal sulcus" should be "STS"

Line 3 from bottom of page 4; "wide spread" should be "widespread".

The last sentence of the first paragraph of page 1; "it is not only...from it as well"; I could not follow this sentence. Please check whether the sentence was as you intended.

Line 8 from bottom in page 16-17; "while matter" should be "white matter".

1st Author Response Letter

### Response to comments from Editors and Reviewers:

Dear Dr. Petkov,

Thank you for considering our manuscript potentially suitable for publication in Current Research in Neurobiology. We are grateful to the three reviewers for their insightful comments and constructive suggestions, which we believe have improved our manuscript. We have now fully addressed all of the comments. In what follows, we provide specific responses to the reviewers' comments, and also highlight the actual edits made in the revised manuscript.

#### Comments from Reviewer 1

General comments

This article provides a sweeping review of recent experiments about the importance of temporal visual cortex in the control of visual attention. The main emphasis is on how recent fMRI and recording experiments in nonhuman primates have provided new evidence that these areas are part of a "temporal attention network" that is not just the recipient of attention control signals but that also plays an important role in coordinating attention with task-related cognitive processes. The tone and treatment of the material is reasonably fair and balanced (although there is a bit of extra emphasis on the "selective tuning" model by John Tsotsos and colleagues), and the authors do a good job of citing older work and putting the new findings into an appropriate historical context.

**Response:** We agree with the reviewer that there was a bit of extra emphasis on the selective tuning (ST) model in the paper (also pointed out by review 2). As the main goal of this review is not to compare attentional models, we have now reduced the emphasis on the ST and also incorporated other classical models whenever applicable (see lines 71, 74, 89-95, 109-118, 254, 385, 396-403, 425-437, 577, 616).

There are a few points that piqued my interest in particular, or that I thought might benefit from some additional explanation, and those are outlined in the major comments below.

To indicate page numbers, I will refer to the pages in the merged pdf document provided for review (i.e., highlights on page 4).

## Major comments

On page 16, you make the point that there is evidence that a TAN exists in both monkeys and humans, based on the observation that similar tasks are able to localize brain regions using fMRI in both species. Is it clear that these regions are indeed homologous, based on other factors (e.g., connectivity, deficits when damaged)? Playing devil's advocate, one might expect that some brain region(s) should be preferentially activated in the ventral stream during these tasks, but that this might occur for very different reasons in monkeys vs. humans (for example, if they used different strategies). If that were the case, then they might not actually be functional homologues. Are there additional reasons for judging these to be homologues, rather than something less conserved?

**Response:** We agree with the reviewer's point. We have removed the word "homologue" and added the following paragraph to the revised manuscript (Lines 476-478):

"Notwithstanding these similarities, future studies investigating connectivity and the causal role of the human TAN in control of attention are needed to ultimately conclude whether the monkey TAN and the human TAN are indeed homologous."

On page 17, you make the interesting comment that the location of these TAN regions might be somehow dictated by the adjacent feature/priority maps, and the mechanistic need for lateralized local connectivity in order for the TAN to accomplish its particular function. There are two points I wonder if you might comment on. First, does this speak to supra-modal attention, and the placement of these regions near other sensory cortices (esp auditory) in addition to being near visual feature maps? Second, does this provide any insight into the different location of the TAN in humans vs. monkeys? Is the TAN in humans surrounded by cortical areas that are needed for some attention capacities that are not present in monkeys? A related point comes up at the end of the article (page 22) when you discuss possible ecological benefits.

**Response:** Thank you for drawing our attention to the auditory domain. This is a very interesting idea which could be tested experimentally. From an ecological point of view, it makes sense that the TAN should be able to accommodate auditory information. We added the following sentences to acknowledge this fact (Lines 522-528):

"When considering that idea that the location of the TAN regions may depend on the adjacent conspicuity maps, to take the advantage of the local information processing mechanisms already available in those areas (such as lateral inhibition, and etc.), one can speculate the TAN can also serve auditory attention as it is also close to auditory cortical areas (Petkov et al., 2006). Previous studies have already shown that auditory attention operates similar to visual attention (Kayser et al., 2005). Indeed, the TAN could be a site of convergence for deploying attention to integrated auditory and visual information and thus further facilitating social interaction processing."

Also, we discussed the location of the TAN in monkeys and humans in the revised manuscript as follows (Lines 460-466):

"When it comes to comparing attentional networks between monkeys and humans, it is noteworthy that the expansion of the temporal cortex in humans during the course of evolution in order to accommodate language, more complex social interactions, and some attention capacities not required

for monkeys might have caused the above-mentioned asymmetrical VAN, its distinct functionality (right hemisphere dominance), and shifting the TAN areas farther away from each other in humans i.e. the monkey GFP and pITd are much closer together than the human GFP and pHIT (see Figure 2).”

On page 19, you make the point about the distinct topography of the TAN and how that would provide surround inhibition. How would this work with objects that are very elongated? This may seem picky, but elongated objects are often very relevant to primates. For example, when leaping through the forest, I might select a branch to grab based on how that particular branch is connected to the trunk of a particular tree. How do you envision that this type of selection takes place?

**Response:** Prior studies of object-based attention have shown that attention spreads along an object, after a spatial cue (originally in Duncan, 1984). In that sense, if the TAN directs attention to part of an elongated object, object-based attentional mechanisms would ensure that the entire object is preferentially processed.

Throughout the article, the experimental findings are placed in a broader theoretical context by references to the 'selective tuning model of attention'. This was ok, but not entirely satisfactory. It is unclear whether you consider the other theories of attention mentioned earlier in the article to be incompatible with the experimental findings, or simply irrelevant (e.g., because their features do not map onto these data). Some additional framing and justification for the focus on this particular model would be helpful. On a related point, does the selective tuning model make any specific predictions that can now be tested? Does the TAN have functional properties that you would only expect if some distinguishing properties of the model were correct? There are some comments along these lines, but they are stated more in terms of findings being 'consistent with' the model, and these consistent observations might be true for a broader range of models and not just the selective tuning model. Please clarify these points.

**Response:** We agree with this point. As previously mentioned, we have now reduced the emphasis on the selective tuning model and also incorporated other classical models whenever applicable.

One of the predictions which we made in the paper according to the ST model, was the role of eccentricity. If the TAN regions form a complete visual field map, activation of one of them suppresses the others. We also proposed that future studies are needed to perform all of these tasks and retinotopic mapping on the same set of subjects to confirm whether the GFP, pITd, and mid-STS areas together form a complete map of the visual field and activation of one of them suppresses the other neighbours.

Minor comments

Page 10. Typo: Rohtblat

**Response:** We fixed the typo (Line 217).

Page 13, top paragraph. The description of the experimental paradigm here was hard to follow. Perhaps a diagram would help clarify, if you think it is worth it.

**Response:** Thanks for noticing this issue. We have now added more details as follows (Lines 324-331):



“Previous studies of the same group showed significant attention-related modulations in monkeys' middle parts of the STS (mid-STS), a cortical area not traditionally linked to attention, during an attentive motion task (Bogadhi et al., 2018). The attention task required detection of a motion direction change in one of the two peripheral random motion stimuli. The color of the central cue was indicative of which stimuli should be covertly attended, and the monkeys had to report the relevant changes detected by releasing a joystick (Bogadhi et al., 2018). In a follow-up study, they showed that responses in the mid-STS and not motion-sensitive areas in the dorsal stream were most strongly attenuated after SC inactivation during the same tasks (Bogadhi et al., 2019).”

Page 13, middle. Has "SC" been defined somewhere?

**Response:** We have now defined the SC where it appears for the first time (Line 67).

Page 14, toward the bottom. This is a very long paragraph and I wonder if it would be better to start a new paragraph when you start discussing "Another common denominator". On that point, not all of the studies referenced involve planning saccades, so it is not clear that this point is indeed common to all of the studies.

**Response:** Thanks for bringing our attention to this issue. In the revised manuscript we mention that all studies on the GFP and pITd include saccadic eye movements (Line 387):

“Another common denominator of the above-alluded studies on the GFP and pITd is that they need to deal with spatial transformations to generate a saccade (Sajad et al., 2020).” This is also now the start of a new paragraph as suggested.

Page 14, last line. Not sure what you mean by "modulatory quantity being attention"

**Response:** By “modulatory quantity” we meant “gain” (see Line 394).

Page 15, first line. Again, not so sure what you mean here. What is the coordinate system for attention-centered, as opposed to eye-centered?

**Response:** We added the following sentences to explain how attention-centered processing might be beneficial at least for invariance object recognition (Lines 396-403).

“An attention-centred coordinate system encodes location of objects relative to the current focus of attention when it does not align with the current gaze location (eye-centered coordinate). Gain modulation provides a basis for the idea that fewer receptive fields that can move around (attention-centered) independent of eye position can be an alternative solution for having too many receptive fields that are fixed at specific retinotopic locations (Salinas & Abbott, 1997; Salinas & Thier, 2000).”

Page 16. "hired"? Perhaps: "now using the same behavioral paradigms as in monkey studies..."

**Response:** This has been fixed it in the revised manuscript (Line 469).

Page 16, about  $\frac{3}{4}$  the way down. Typo: "findings"

**Response:** This has been fixed it in the revised manuscript (Line 487).

Page 17, First question "what is the relationship between feature selectivity..." I do not fully understand what you mean by this, or why the answer would be important. Please clarify.

**Response:** We just removed this sentence as we found it irrelevant.

Page 20, 9 lines from bottom. Typo: "supports"

**Response:** This has been fixed it in the revised manuscript (Line 591).

Page 20, 8 lines from bottom. "white" matter?

**Response:** This has been fixed it in the revised manuscript (Line 592).

Page 21, top. You don't say much about connectivity of mid-STS. Are there also inputs from pulvinar and superior colliculus?

**Response:** We added some information about the mid-STS connectivity (Lines 599-603).

"Cortex around the mid-STS has been shown to connect visual areas such as V2, V3, MT, and MST, to more anterior parts of the STS (Boussaoud et al., 1990). The mid-STS is also connected with attention-related areas such as FEF (Boussaoud et al., 1990) and the pulvinar (Kagan et al., 2021). Hence, one can conclude that the mid-STS is the central node of a pathway connecting cortical motion processing (starting from MT) with subcortical and cortical attentional control areas."

## Comments from Reviewer 2

General comment:

1) In this review paper, the authors discuss the idea of a Temporal Attention Network (TAN), consisting of the posterior dorsal inferior temporal cortex (pITd), the gaze following patch (GFP), and the mid-superior temporal sulcus (mid-STS). Evidence is presented from non-human primates (NHPs) that these brain regions respond to attentional demands, are connected with the dorsal and ventral attention networks, as well as various visual areas, and are implicated in social behavior. Overall, the idea of a TAN is well argued and timely considering recent NHP studies. However, while it is useful to incorporate theoretical/computational models of attention, the reader would be better served by a more equitable coverage of existing models, rather than focusing on models from one lab. Further, Figure 1 could be reworked to enhance the narrative; and the social interactions section could be better substantiated with more published work. Specific comments to accordingly help with revisions below.

**Response:** Thank you for your suggestions. The main goal of this review is not to compare attentional models, but we agree that it might be better to have a more balanced review of the other influential models. In the revised manuscript, we have reduced the emphasis on the ST and also incorporated other

classical models whenever applicable ((see lines 71, 74, 89-95, 109-118, 254, 385, 396-403, 425-437, 577, 616). We have removed Figure 1 and also enhanced the narrative on social interactions.

Specific comments:

2) RE: Visual attention section, 4th paragraph: "In addition to the premotor theory of attention, several other theories such as biased competition [4,33], selective tuning [34,35], and the rhythmic theory of attention [36]...Nevertheless, here we briefly review the concept of the selective tuning model [37] which is relevant for temporal cortex participation in attentional control." As the authors point out, there are a number of theories of attention, e.g., Reynolds and Heeger (2009, Neuron), Itti and Koch (2001, Nat Rev Neurosci), Olshausen et al. (1993, J Neurosci), Bundesen et al. (2005, Psychol Rev) in addition to those mentioned. A number of these theories are "relevant for temporal cortex participation in attentional control". Rather than only focusing on the selective tuning model, it would be more useful to the reader to rework this paragraph, and the rest of the review, to better reflect the other contributions as well. One possibility is to rephrase such that the multiple levels, "winner take all" mechanisms, etc, are common aspects of multiple models.

**Response:** We have now added those models that might related to the findings on the TAN.

Lines (89-95) and (109-118):

"Another computational model which is able to explain seemingly disparate experimental findings in the domain of visual attention is the normalization model of attention (Reynolds & Heeger, 2009). In this model, neural activity (designated as "stimulus drive") is integrated with an external "attention field" and a "suppressive field", that pools responses to non-preferred stimuli and unattended locations, which is used as in normalization. According to this model, attention modulates the strength of normalization which appears to operate at all stages of the visual system regardless of what biophysical mechanism it entails."

"Relatedly, a theory of visual attention (Bundesen, 1990) proposes that each stimulus that reaches the short-term memory earlier than others can be represented and recognized later. Each stimulus' individual processing speed is affected by its attentional weight which, in turn, are affected by the task relevance and saliency of the stimulus' features (Bundesen, 1990; Bundesen et al., 2005). Bundesen and colleagues proposed that dynamic remapping of receptive fields of cortical neurons is the basis for setting the weights which are used for reallocation of attention i.e. the more neurons allocated to an object the higher the attentional weight of the object (Bundesen et al., 2005). The neural implementation of this model requires two successively computed forms of object representation (Bundesen, 1990), an elementary visual feature representation which are not accessible for goal directed actions (also called proto-objects (Schneider, 2013)), and a visual working memory representation (also called visual tokens (Schneider, 2013))."

3) RE: Temporal cortex participates in attentional control section, Figure 1. To me, Figure 1 does not significantly enhance understanding of early vs late attentional selection beyond what is in the text. Instead, it may be more useful to either show data from the discussed paper by Rohtblat and Pribram or other relevant studies, or provide a toy example of what the neural responses themselves look like

during early and late selection (e.g., the time courses of neural activity surrounding the stimulus and response).

**Response:** We agree with the review that the Figure 1 does not add any significant information beyond the text. This was also raised by review #3. In the revised manuscript we have removed Figure 1.

4) RE: "Cognitive programs". The hypothesis of "cognitive programs" as proposed by Tsotsos and Kruijne (2014, *Frontiers*) is a useful approach to understanding executive functions and the control of visual attention. However, there are other relevant frameworks here, e.g., Bundesen et al. (2005, *Psychol Rev*), Miller and Buschman (2013, *Curr Opin in Neurobiol*), Botvinick et al. (2009, *Cognition*), etc. It would be more useful to the reader to rework the text covering "cognitive programs" to better reflect other relevant contributions to cognitive control as well.

**Response:** We agree with the reviewer. We have integrated those relevant papers to better reflect how the TAN might contribute to cognitive control (425-437):

“As discussed in Section 1, the theory of visual attention and its neural implementation proposed (Bundesen, 1990; Bundesen et al., 2005) assumes that there two successive neural representation of objects, a first one which is not accessible for goal directed action (proto-objects) and a second visual working memory (visual tokens) (Schneider, 2013). It is plausible to speculate that the TAN might indeed be corresponding to visual tokens, preparing the object to be acted on. This notion gets further support from the fact that neurons in the pITd were not representing visual motion or many of the GFP neurons were not representing faces (Ramezanzpour & Thier, 2020; Stemmann & Freiwald, 2019). It would be interesting to test neurons in the TAN in working memory tasks more systematically in future studies. Relatedly, the prefrontal-like responses of the TAN (such rule selectivity and context dependency of the GFP neurons) may suggest that the TAN may correspond to option identifier in hierarchical reinforcement learning models that route option-specific policies corresponding to stimulus-response pathways (Botvinick et al., 2009). Hierarchical reinforcement learning extends the classical models by assuming the learning agent’s actions can be made of reusable subroutines or skills (Botvinick et al., 2009).

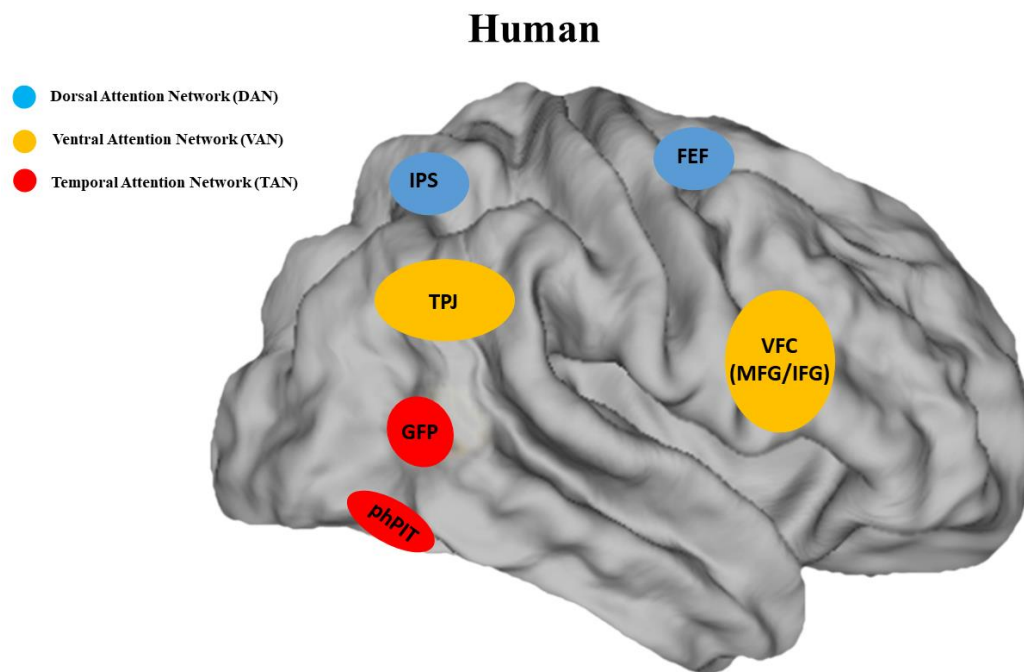
5) RE: the section "What do the TAN regions have in common". This section presumes that the IT cortex is involved in both attentional processes and broader executive functioning. However, the fact that behavioral tasks used have an executive component does not necessarily mean the TAN is involved in executive functioning itself. Likewise, while the disruption of prefrontal cortical activity from IT cooling suggests the region is involved in attentional processing, it does not imply the disruption is due to disrupting "cognitive programs" as described in the text. Please elaborate with more evidence that "the neural circuits in the TAN are not just passive receivers of attention signals, but they also significantly contribute to executive control of visual attention and implementation of cognitive programs during complex behaviors." Otherwise, it might be more appropriate to better balance the hypotheses about the TAN with the contributions of prefrontal and parietal cortex to executive functioning. This also applies to the conclusions section of the paper.

**Response:** In the revised manuscript we have removed this sentence as it was an unnecessary duplication of the conclusions section. There are several reasons that suggest the TAN significantly contributes to executive control of visual attention such as (1) there are neurons in the GFP which discriminate between abstract rules. When the discriminatory power of these neurons is reduced the monkeys make more errors during gaze following. (2) Most of neurons in the area pITd are not feature

selective and only signal the animal's state of attention and microstimulation of this area deploys attention and directly influences the animal's performance. (3) Pharmacological inactivation of the area mid-STS induce spatial neglect-like behavior. We agree that this does not mean the TAN is independently operating and the TAN is part of the broader executive function network including prefrontal and parietal areas.

6) When describing the human correlates of the TAN in fMRI studies (page 12 on my copy), the authors mention the areas are clearly far from the TPJ but do not describe the areas of the human TAN in detail. Please describe or show the locations of the human TAN.

**Response:** We have now added the following figure (Figure 2, in the revised manuscript) which demonstrate the human TAN.



**Figure 2. Cortical attention networks in humans.** Blue: The dorsal attention network (DAN) (Corbetta et al., 2008; Corbetta & Shulman, 2002; Vossel et al., 2014), red: the temporal attention network (TAN) (Marquardt et al., 2017; Sani et al., 2021), and orange: the ventral attention network (VAN) (Corbetta et al., 2008; Corbetta & Shulman, 2002; Vossel et al., 2014). IPS: intraparietal sulcus; FEF: frontal eye field; GFP: gaze following patch; phPIT: putative human posterior inferotemporal area; TPJ: temporoparietal junction; VFC: ventral frontal cortex; MFG: middle frontal gyrus; IFG: inferior frontal gyrus.

7) RE: the section "Implications of active vision in temporal cortex for social interactions" is reliant on "anecdotal reports of the neurons in the STS representing others' actions [181]". It also relies on unreferenced assumptions of parsimony and ecological benefit about social cues and representations in the temporal cortex. Currently, this seems quite speculative. I might suggest providing additional evidence of social-related activity in the temporal cortex. For example, single- and multi-unit recordings in humans have reported mirror neurons and other neurons related to action perception in temporal

cortex (Mukamel et al., 2010, *Current Biology*). Further, a number of other brain areas have been shown to constitute social neural networks, e.g., premotor and posterior parietal cortex (Rizzolatti and Sinigaglia, 2010), orbitofrontal cortex (Azzi et al., 2012), anterior cingulate cortex (Chang et al., 2013; Yoshida et al., 2012; Haroush and Williams, 2015), etc. How would the TAN relate to these other areas? Additionally, similar to point 5 above, why is it necessary that these computations take place in the TAN and not in other areas of the frontal and parietal lobes?

**Response:** Thanks for this suggestion. There are studies, including (Mukamel et al., 2010, *Current Biology*) which you mentioned, which have shown involvement of the temporal cortex regions in action observation and/or action execution. How exactly would the TAN relate to these areas and those others in the frontal or parietal cortices you mentioned is not clear at the moment, although they may be interconnected to support broader social processing. In the text, we have further explained how the TAN could be beneficial for such social functions and what its advantage over frontoparietal attention areas might be. The following paragraphs explain our thoughts (Lines 631-676):

“We hypothesize that the participation of the TAN regions in attentional control and cognitive programs is also beneficial for action understanding. In order to arrive at a complete interpretation of the given social context, we need to flexibly switch between various cues and actions and integrate the information collected. Hitherto, the neurophysiological principles that orchestrate ensembles of neurons to flexibly link these cues to generate a meaningful and dynamic percept of other’s actions have been mostly studied in the context of mirror neurons (Rizzolatti & Craighero, 2004). Nevertheless, there are several studies showing that various regions in the temporal cortex contribute to the perception of other’s actions in both monkeys and humans (Iacoboni et al., 2001; Kilintari et al., 2014; Nelissen et al., 2006, 2011; Perani et al., 2001; Pierno et al., 2006), similar to what has previously been found in the premotor cortex (Rizzolatti & Craighero, 2004). Importantly, some of these areas even show activity during execution of the same actions (Kilintari et al., 2014). While some of these areas such as the STP, which encompasses regions TPO, PGa and IPa, are active during action observation and execution only when actions are visible (Kilintari et al., 2014), some other areas such as MT, MST, FST, remain active even if actions are performed in darkness or if they are invisible to the performer (Gazzola & Keysers, 2009; Kilintari et al., 2014). These findings suggest that mirror-like responses found in the motion complex part of the temporal cortex (MT, MST, FST) may reflect visual imagery from the actor’s point of view (Kilintari et al., 2011, 2014) which rely on top down efferent signals from prefrontal and parietal cortices. Interestingly, at least the mid-STS, a member of the TAN, partially overlaps with FST and parts of the TPO.

In contrast to the temporal cortex, other brain regions such as premotor and posterior parietal cortex (Rizzolatti & Sinigaglia, 2010), orbitofrontal cortex (Azzi et al., 2012), anterior cingulate cortex (Chang et al., 2013; Haroush & Williams, 2015; Yoshida et al., 2012) have so far been considered to play a more important role when it comes to social action monitoring, action observations, and action execution. It remains to be investigated how the TAN and other areas of the STS which showed mirror-like responses functionally relate to these areas in the parietal and frontal cortices.

How can the TAN contribute to action understanding during social interactions? Primates as a social species need to process and direct attention based on social cues as much as nonsocial ones (such as a

flashing red light). At a lower level, attention has been shown to play an important role in binding visual features such as color and motion into an object representation (Bodelón et al., 2007; Perry & Fallah, 2014; Treisman & Gelade, 1980). Hence it is parsimonious to assume that attention might also be necessary to bind different social cues provided by others in order to generate a unified action. Take gaze following as an example in which attention should be constantly paid to the other person's face in order to be able to detect abrupt changes in their gaze direction, head movements, and finally the object they fixate on. As described previously, the processes which are needed to perform these actions rely on cognitive programs to which the temporal cortex contributes. Consistent with the selective tuning model of attention, temporal cortex, as an intermediate level in the visual hierarchy, can reduce interference among other elements by operations such as pruning away task irrelevant information. The idea that TAN could bind several representations of social cues into one unified action gets further support from a theory by Keysers and Perrett that hypothesizes events which systematically follow each other could be associated in Hebbian ways across various modalities such as visual and motor domains. They further proposed that there are action codes which integrate visual effects with motor commands and it is possible that Hebbian learning retrieves the STS representation of actions during executions (Keysers & Perrett, 2004).

Why is the temporal cortex a good candidate for implementing the above operations? The essential elements of social interactions such as faces, body parts, and biological motion are indeed already represented in the temporal cortex. Hence implementing attention control signals and cognitive programs at the level of temporal cortex is ecologically beneficial because the local information processing mechanisms already available in these areas (such as lateral inhibition, surround suppression, etc.) can be recruited for binding social cues, flexibly switching between them, and implementing them into attentional control."

Minor comment:

8) From the main text: "Since the GFP is very close to the pITd, one might expect that their connections should not be drastically different than the pITd." Possibly, but not necessarily so, e.g., dorsal and ventral LIP have distinct connectivity patterns. Perhaps rephrase the quoted sentence.

**Response:** We agree. In the revised manuscript we replaced this sentence with (Lines 595-598):

"Connectivity of the functionally defined GFP has yet not been studied. Nevertheless, purely anatomical studies have shown that in addition to reciprocal connections to the early visual areas, the GFP receives input from a subcortical pathway including the pulvinar (Kaas & Lyon, 2007) and superior colliculus (Bogadhi et al., 2019, 2020) and in turn projects to the interparietal sulcus, likely area LIP (Baizer et al., 1991)".

### Comments from Reviewer 3

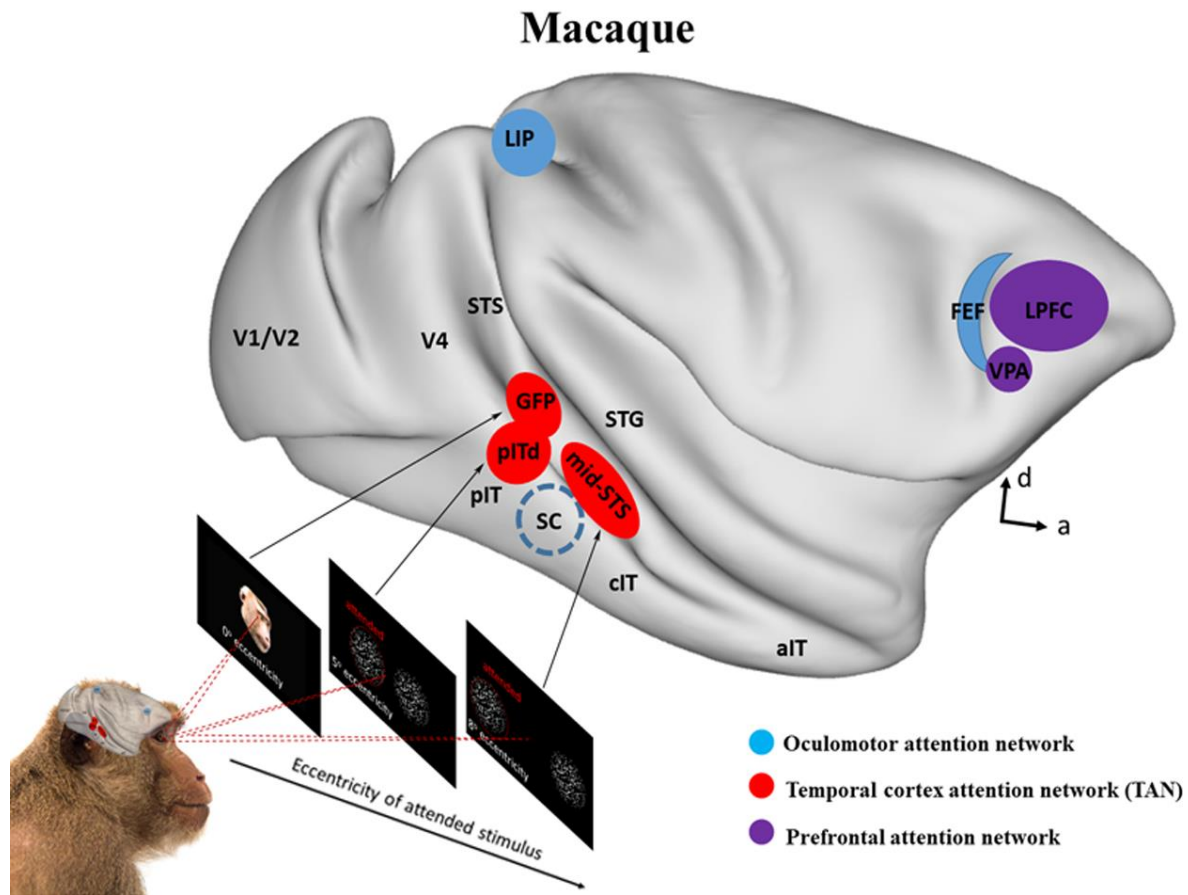
This review article summarized the literature on the possible involvement of the temporal cortex in control of attention. This is a timely opinion because traditionally the temporal cortex has been considered as the center for passive object recognition, however recently accumulating evidence supports that the temporal cortex is also actively involved in control of object-based attention. In general, the manuscript comprehensively summarizes the current status of the field, but I also have to raise several issues, which are unclear and the authors have to reconsider.

**Response:** Thank you for your interest in our manuscript. In the revised manuscript, we have tried to address your comments as good as possible.

Figures 1 and 2 do not well match the descriptions in the text. I recommend the authors to reconsider the relationship between Figure 1 and the text. Figure 1 is explained in the initial half of the 2nd paragraph of page 6. However, the text (especially, the part "They showed initially the neural responses ..... filtering via the IT cortex [119] (see Figure 1)") does not seem to follow the content of the figure. I recommend to revise the text, or the content of Figure 1. As for Figure 2, there are many names of brain areas (such as MTC, STG, STS, IT, pIT, cIT, aIT, VPA, GFP...) and pathway (such as TAN), however to many of the readers, their anatomical locations are not obvious. Therefore, I recommend the authors to use a figure which explains the anatomical locations and functions of the areas described in the text. In this aspect, the authors intention of Figure 2 is not clear to me. Intention of 2 right black panels at the bottom is not clear to me. Thus, I think Figure 2 needs to be revised to give sufficient information described in the text to the readers.

**Response:** We agree with the review that the Figure 1 does not add any significant information beyond the text. This was an issue also raised by review #1. In the revised manuscript we have removed Figure 1. Moreover, we added the name of the mentioned brain areas (except for MTC which can not be shown on a lateral view) to Figure 2, which now becomes Figure 1 in the revised manuscript (see below).





**Figure 1.** Oculomotor, prefrontal and temporal cortex areas involved in the control of attention. Blue: The oculomotor system priority maps [49], red: The temporal cortex attention network (TAN) [43,45,47], and purple: the prefrontal control areas [118,149]. The presentation of the visual stimuli that required to be attended at various eccentric locations might have shifted the locus of attention control signals in the posterior-middle temporal cortex. Note that the locus of priority maps are approximate locations based on coordinates found in the corresponding original papers. To confirm the exact relationship between attentional foci in the temporal cortex and the type and eccentricity of stimuli, future studies should carry out mapping these areas in the same animals.

The authors need to be careful about font usage. The texts are bold in some cases or written in different fonts.

**Response:** We have fixed this issue in the revised manuscript.

Typos (?);

The first line of 2nd paragraph of page 4; "superior temporal sulcus" should be "STS"

Line 3 from bottom of page 4; "wide spread" should be "widespread".

The last sentence of the first paragraph of page 1; "it is not only...from it as well"; I could not follow

this sentence. Please check whether the sentence was as you intended.  
Line 8 from bottom in page 16-17; "while matter" should be "white matter".

**Response:** Thanks for spotting these typos. We have fixed them in the revised manuscript (Lines 151, 170, 592).

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Accept Letter

Dear Dr. Ramezanpour,

Thank you for submitting your manuscript to Current Research in Neurobiology.

I am pleased to inform you that your manuscript has been accepted for publication.

My comments, and any reviewer comments, are below.

Your accepted manuscript will now be transferred to our production department. We will create a proof which you will be asked to check, and you will also be asked to complete a number of online forms required for publication. If we need additional information from you during the production process, we will contact you directly.

We appreciate and value your contribution to Current Research in Neurobiology. We regularly invite authors of recently published manuscript to participate in the peer review process. If you were not already part of the journal's reviewer pool, you have now been added to it. We look forward to your continued participation in our journal, and we hope you will consider us again for future submissions.

*CRNEUR* aims to be a unique, community-led journal, as highlighted in the [Editorial Introduction](#). As part of this vision, we will be regularly seeking input from the scientific community and encourage you and your co-authors to take the [survey](#).

Kind regards,

Christopher I. Petkov  
Editor in Chief  
Current Research in Neurobiology

Editor and Reviewer comments:

Reviewer 1: The authors have appropriately revised the manuscript. No further comments.

Reviewer 2: The authors have addressed my comments.

Reviewer 3: I read through the revised manuscript and found that the authors appropriately responded to my comments on the original version, and also to the comments from the other reviewers, such as adding the relevant literature and arguments. I have no more comments to the revised manuscript.

----- *End of Review Comments* -----