Attention is Amplification, not Selection

Peter Fazekas and Bence Nanay

Abstract

The paper argues that recent empirical findings and theoretical models shed new light on the nature of attention. According to the resulting Amplification View, attentional phenomena can be unified at the neural level as the consequences of the amplification of certain input signals of attention-independent perceptual computations. The paper demonstrates that this way of identifying the core realiser of attention is able to evade standard criticisms often raised against sub-personal accounts of attention. Moreover, the paper argues that this approach also reframes our thinking about the function of attention by shifting the focus from the function of selection to the function of amplification.

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1 Introduction

Attention plays a key role in recent discussions concerning agency (Wu [2011a], [2011b], [2014]; Jennings and Nanay [2016]), reference (Campbell [1997], [2002]), and especially consciousness (Chalmers [2004]; Block [2010]; Nanay [2010]; and also, for example, Koch and Tsuchiya [2007]; Cohen et al. [2012]), and even in distant fields like aesthetics (Nanay [2015])—despite the fact that issues related to the nature of attention are far from being settled.

 Psychologists and neuroscientists have identified manifestations of attention at almost every stage of the perceptual and cognitive system (Serences and Kastner [2014]), and discovered vastly different varieties of how attention affects neural processing (Carrasco [2011], Treue [2014]). These observations led many to seriously question whether there is any common core function underlying the effects and manifestations of attention, and whether different attentional phenomena can be seen as the product of a unitary mechanism (for a review and taxonomy, see Chun et al. [2011]). This gives rise to the so-called Disunity Problem (Watzl, [2011b]) that claims that since attention at the neural level is highly disjunctive, finding a unified characterisation at this level of enquiry is particularly unlikely (Wu [2014], Taylor [2015], Watzl [2017]).

 As philosophers frequently argue, neural level—reductive—accounts of attention face another problem as well. According to this so-called Overgeneralisation Problem (Watzl, [2011b]), the mechanisms and functions that usually correspond to attention at the level of brain processes often occur in the absence of attention (i.e. when the subject is not attending), and thus these alleged neural bases are not sufficient for, and cannot realise attention (Mole [2011a], Wu [2014], Watzl [2017]). The motivation behind the Overgeneralisation Problem is the idea that attention, just like agency, or mentality in general, is a personal level phenomenon, and as such it can only be attributed to persons (psychological subjects) and not to sub-personal systems, i.e. parts of persons (see Wu [2014]). Consequently, most of the major contemporary philosophical approaches to attention aim to give a personal level account (Smithies [2011]; Watzl [2011a], [2011b], [2017]; Jennings [2012]; Wu [2011a], [2011b], [2014]). However, there is no consensus with regard to the nature of attention in the philosophical literature either. Some claim that the nature of attention is ultimately determined by the fact that attention is selective and the question is how we characterise the relevant kind of selection (see Wu [2011a], [2011b], [2014] arguing for a selection for action, or Jennings [2012] arguing for a subject-directed mental selection view). Others try to capture what attention is in terms of its relationship to consciousness (Watzl [2011a] claims that the crucial feature of attention is how it structures the stream of consciousness, whereas Smithies [2011] claims that attention is rational-access consciousness), or, as it has recently been argued, in terms of how attention manages an agent’s priority structures (Watzl [2017]). Still others think that attention is not a product of a mechanism but rather a manner of occurrence, i.e. an adverbial phenomenon (Mole [2011a], [2011b]; Koralus [2014]).

 Our aim here is to provide a novel answer to the ‘what is attention’ question. In what follows, we will argue that recent empirical discoveries and theoretical models shed new light on the nature of attention. On the basis of these results we will argue that contrary to the received view, it is possible to provide a sub-personal account of attention that is able to unify attentional phenomena at the neural level. In a nutshell, the account we propose claims that the diverse neural effects of attention are all brought about by a particular ‘not-stimulus-triggered’ amplification of stimulus-specific inputs of certain canonical neural computations. We emphasise not-stimulus triggered amplification because the effects attention has on neural representations can be evoked in a purely stimulus driven way, independently of attention, due to built-in, attention independent perceptual mechanisms that, driven by changes in the physical features of a stimulus, can generate the effects in question. Attention capitalises on this built-in capacity to modulate neural representations by amplifying the input of these mechanisms — mimicking local manifestations of changing stimulus feature values, without actual physical changes (see Section 3). After formulating this Amplification View of attention, we will answer the challenge raised by the Disunity Problem by demonstrating that according to a growing body of empirical findings and modelling studies this very mechanism gives rise to a broad spectrum of attentional phenomena (Section 4.1). Next, we will defend the Amplification View against the Overgeneralisation Problem by arguing that what the Amplification View describes is the core realiser of personal level attentional phenomena. Personal level features of attention are products of different broad sub-personal mechanisms (total realisers) that all share a common part (the core realiser) and the Amplification View picks out this common part (Section 4.2).

 A consequence of the Amplification View is that we need to discard a widely held assumption in the attention literature, namely, that the most fundamental function of attention is selection. This is a widespread consensus that is dominant both in the neuroscience (Petersen and Posner [2012]) and the psychology (Carrasco [2011]) literature (for a similar claim, see Wu [2014], p.12). It is also our aim here to challenge this core commitment of the attention literature. In what follows, we will introduce our Amplification View as a superior alternative to this traditional Selection View. We should reframe our thinking about the function of attention in terms of amplification as selection is, in fact, an attention-independent effect of perception.

2 What is Attention?

Setting the stage, this section overviews the major behavioural and neural effects of attention, and discusses the motivations for thinking that attentional phenomena cannot be unified at the neural level.

2.1 Effects of attention at the psychological level

Subjectively, the most profound effect of attention is its capacity to bring the attended stimulus into the forefront of our conscious experience while unattended stimuli fade into the background, and even can be filtered out entirely (Watzl [2011a], [2017]). A classical empirical study investigating this effect is Colin Cherry’s dichotic listening paradigm (Cherry [1953]). Cherry simultaneously played competing speech inputs into the two ears of participants, who were instructed to pay attention to and repeat one stream of speech input while ignoring the other. Cherry found that participants were unable to recall what was played in the unattended ear; in fact, they did not even notice significant changes in the input, like switching to another language, or playing the message backward. Much of the psychological research on attention in the 1960s and 70s focused on determining how and exactly where in the perceptual processing stream such filtering occurs (Broadbent [1958], Deutch and Deutch [1963]; see also Lavie [1995], Prinz [2012])

 While the dichotic listening paradigm informs us about what happens with unattended stimuli, it tells little about what happens with the attended stimulus. Michael Posner’s cuing paradigm revealed that it was more than merely admitting attended signals through for further processing: attention increases processing efficiency (Posner [1980]; Posner et al. [1980]). Participants, fixating on a central point, were asked to detect stimuli briefly flashed either to the left or the right of fixation. Each trial started with the presentation of a cue at the fixation point, which in half of the trials was followed by the presentation of the target. Three different cues were used: a plus sign, indicating that it was equally likely that the target would appear at either sides a left arrow, and a left and a right arrow, in which case it was four times as likely that the target would appear on the left/right than on the other side (75% valid cue, 25% invalid cue). In trials in which the cue was the plus sign, target detection rates were around 60% and reaction times around 250-300 ms. In valid cue trials target detection rates increased to 80%, and reaction times were 20-30 ms faster. In invalid cue trials target detection rates dropped to 50%, whereas reaction times were 20-30 ms slower than in the neutral trials. That is, focusing attention on a region of the visual field enhances the detection of stimuli presented in the attended region, and speeds related reaction times compared to cases where attention is distributed over larger regions (see also Castiello and Umiltà [1990]; Eriksen et al. [1990]; Castiello and Umiltà [1992]).

 In recent years, it has been demonstrated that attention’s role in increasing processing efficiency manifests itself at each and every stage of perception. For example, at low levels of stimulus processing attention enhances spatial resolution: subjects are able to discriminate finer details when they are attending to a given location compared to cases when they are attending elsewhere (Yeshurun and Carrasco [1998]; Carrasco and Yeshurun [2009]). Attention also increases perceived contrast: for subjects fixating on a black square flanked by two Gabor patches with different contrast levels (22% and 28%), covertly attending to the patch with the lower contrast level makes the contrast of the two patches indistinguishable—i.e. attention makes a 22% contrast patch look like an unattended 28% contrast patch (Carrasco et al. [2004]). Attention similarly affects other properties as well: it increases perceived gap size (Gobbell and Carrasco [2005]), apparent saturation (Fuller and Carrasco [2006]), motion coherence (Liu et al. [2006]), stimulus size of a moving object (Anton-Erxleben et al. [2007]), flicker rate (Montagna and Carrasco [2006]), and speed (Fuller et al. [2009]).

2.2 Effects of attention at the neural level

As recent studies have demonstrated, attention achieves its personal level (phenomenal and behavioural) effects by modulating information processing at the neural level (Carrasco [2011]; Anton-Erxleben and Carrasco [2013]).[[1]](#footnote-2)

 Sensory neurons have three crucial characteristics: they respond to the stimulation of only a special region of the retina (the so-called receptive field of the neuron); they are sensitive only to a specific kind of stimuli (say, the orientation of an edge); and have a preferred value (say, a specific orientation) such that the response function, the so-called tuning curve, of the neuron peaks around its preferred value. That is, when, a single oriented edge appears in the receptive field of an oriented edge sensitive neuron, the neuron will respond with an increased firing rate (compared to baseline activity) depending on how close the orientation of the edge is to the preferred orientation of the neuron, such that the preferred orientation triggers the most rapid firing.

 When attention is allocated to a region of space (spatial attention), it modulates the tuning curve of those neurons that are sensitive to the stimulus features present in the attended region by increasing the activity of the neuron such that the same stimulus-feature evokes increased firing rate when attended compared to cases when it is unattended. The result is if attention multiplied the overall neural response function of the population of neurons encoding the attended feature by a constant factor (see, McAdams and Maunsell [1999]; Fries et al. [2001]; Carrasco [2011], [2014]).

 When attention is allocated to a specific feature value (feature-based attention), it modulates the tuning curve of those neurons that are sensitive to the specific stimulus feature such that the closer the preferred value of a neuron is to the attended value the more its firing rate will be increased—regardless whether the neuron’s receptive field coincides with the actual focus of spatial attention. The result is an increased population code that is also sharpened around the attended feature value (Martinez-Trujillo and Treue [2004]; Maunsell and Treue [2006]).

 When there are two stimuli in the receptive field of a neuron, then allocating attention to one of them decreases the effect the other has on neural signalling—as if attention reduced the size of the receptive field around the attended stimulus, and thus the unattended one fell outside the receptive field (Moran and Desimone [1985]). When an oriented edge with preferred orientation appears in the receptive field of an oriented edge sensitive neuron, the neuron produces a strong response. When an oriented edge with a non-preferred orientation appears in the receptive filed, the neuron produces a weaker (but still increased compared to baseline) response. If, however, both stimuli are present in the receptive field, then the neuron’s response is in between the two individual responses—that is, responses corresponding to the two individual stimuli do not add up when the two stimuli appear together, instead, the neuron produces a normalised response (Carandini et al. [1997]; Reynolds and Desimone [2003]). What experimental results show, is that attentional modulation shifts this normalised response towards responses that correspond to one of the two single stimulus conditions. If attention is directed to the preferred orientation when both stimuli are present, the neuron produces a stronger response than its normalised response in the no-attention condition, i.e. its response characteristics get closer to the case when only the preferred orientation is present. Similarly, if attention is directed to the non-preferred orientation, then the neuron produces a weaker response than it would without attentional modulation, i.e. its response becomes more similar to the case when only the non-preferred orientation is present. That is, attending to the preferred stimulus increases, whereas attending to the non-preferred stimulus decreases neural activity as if the receptive field shrunk or got remapped around the attended stimulus (Moran and Desimone [1985]; Chelazzi et al. [2001]).

2.3 The Disunity Problem

Since the multiplicative gain mechanism enhances the neural representation of the attended stimulus, whereas the mechanism of receptive field remapping favours specific stimuli while disregards others, it is tempting to interpret these mechanisms as the neural level implementations of how attention enhances stimulus processing and how attention selects some stimuli while filtering others out (see Wu [2014], pp.54-58). As a result, the significant difference between these mechanisms is often cited as an empirical reason for thinking that attentional phenomena cannot be unified at the neural level.

 A neural level unificatory account seems even more ambitious once one realises that the neural effects of attention introduced in the previous section are only the most widely discussed ways in which attention modulates neural behaviour. In fact, attention has an even more diverse and more nuanced set of effects at the neural level.

 For example, under different conditions the gain mechanism that increases the tuning curve of populations of neurons encoding attended features has different effects on the contrast-response function (describing how the neural response changes with different values of stimulus contrast). Under some conditions a so-called contrast gain can be observed shifting the contrast-response function uniformly towards lower contrast levels (Martinez-Trujillo and Treue [2002]; Reynolds et al. [2000]). Under other conditions a so-called response gain can be observed shifting the contrast-response function multiplicatively towards higher response levels (McAdams and Maunsell [1999]). Under still other conditions the effects are intermediate between a contrast gain and a response gain (Williford and Maunsell [2006]).

 The modularity effects of attention are not even restricted to enhancing neural activity—attention also actively suppresses neural processing. For instance, it has been observed that attention decreases contrast sensitivity and acuity compared to the baseline at non-attended locations (Pestilli and Carrasco [2005]; Pestilli et al. [2007]; Montagna et al. [2009]). It has also been observed that attention creates a suppressive zone around the focus of attention both in physical space and in feature-space resulting in ‘Mexican hat’ style neural response profiles with an excitatory centre and an inhibitory surround (Maunsell and Treue [2006]; Störmer and Alvarez [2014]).

 Moreover, changing the response strength is not the only modulatory effect of attention on neural behaviour. Attention also affects the response correlation between pairs of neurons—depending on the context, attention either increases or decreases the spike-count correlation between neurons. In fact, as it has recently been argued, this attentional effect is far more important with regard to modulating the quality of neural representations than changes in response strength (Verhoef and Maunsell [2017]).

 The Disunity Problem is the problem that no single theoretical model could previously explain all these vastly different effects of attentional modulation, and thus a neural level unificatory account of attention seems to be clearly out of sight (Wu [2014], Watzl [2017]). Our aim is to argue that the Amplification View provides an elegant solution to the Disunity Problem.

3 The Amplification View

In this section, we will review neural level findings, models and hypotheses that point towards a novel interpretation regarding the nature of attention.

3.1 A common mechanism

We have seen in Section 2.2 that sensory neurons that are sensitive to vertical edges respond to vertical edges with the strongest signal and to horizontal edges with the weakest signal. If an edge is attended, then the neuron responds with an increased firing rate (McAdams and Maunsell [1999]).

 Note, however, an important fact about the functioning of these orientation sensitive neurons. The same oriented edge in the receptive field of the neuron with a higher contrast level evokes a stronger response (even if attention is directed elsewhere). That is, the responses of orientation sensitive neurons are modulated not just by stimulus orientation, but by stimulus contrast as well. There is a built-in mechanism responsible for the modulation of the neuron’s behaviour as a function of the contrast of the stimuli the neuron is sensitive to.

 Even more importantly, as it has been empirically demonstrated (Reynolds et al. [2000]), the effects that the allocation of attention has on a neuron’s behaviour is similar to the changes that would occur if the neuron was triggered by a stronger afferent signal that normally corresponds to a higher stimulus contrast. That is, attention achieves its modulatory effect by triggering a built-in mechanism that is originally responsible for the generation of increased firing rates as a response to higher stimulus contrast by increasing the strength of the presynaptic signal itself (Reynolds et al. [2000], p.710).

 Next, consider the mechanism of receptive field reduction. When two stimuli appear together in a neuron’s receptive field, the allocation of attention alters the neuron’s normalised response: attending to one of the stimuli will shift the normalised response closer to the individual response corresponding to the attended stimulus. That is, the allocation of attention decreases how much the unattended stimulus is able to drive neural behaviour (Moran and Desimone [1985]).

 However, just as the gain mechanism discussed above, receptive field reduction can also occur without the allocation of attention. If the contrast of, say, the stimulus with the orientation closer to the preferred value increases, then the neuron’s response will increase as well, i.e. it will shift towards the corresponding individual response—and vice versa (Carandini et al. [1997]). That is, again, there is a built-in mechanism responsible for the generation of a normalised response to two stimuli concurrently present in the receptive field as a function of the contrast-levels of the stimuli in question. And, again, attention only capitalises on this built-in mechanism, i.e. triggers it, by increasing the strength of the presynaptic signal corresponding to the attended stimulus (Reynolds and Desimone [2003]; Reynolds and Chelazzi [2004]).

3.2 Input amplification triggering built-in mechanisms

The moral of the previous subsection is that seemingly different manifestations of the allocation of attention, like increased firing rate and receptive field reduction—the distinctness of which has been fuelling the claim that attentional phenomena cannot be unified at the neural level—can, after all, be interpreted within a single framework as the consequences of the same underlying mechanism. This mechanism consists in the amplification of a presynaptic signal (corresponding to, say, the contrast level of an oriented edge stimulus), which then, depending on the actual circumstances (i.e. whether there is one or two stimuli in the receptive field of the neuron in question) results in different neural behaviour.

 This moral is further supported by the so-called Normalisation Model of Attention, a particularly interesting theoretical approach that, motivated by the empirical findings introduced in the previous section, aims to uncover computational mechanisms that could explain the similarities between the effects of changes in stimulus contrast and the effects of allocating attention.[[2]](#footnote-3) According to a specific interpretation of this model (Reynolds and Heeger [2009]; for an alternative see Lee and Maunsell [2009]), neural output is jointly determined by three distinct factors: stimulus features, the operation of an ‘attentional field’—that exerts its effects by multiplying the local excitatory input of the neurons in question,—and built-in input processing mechanisms that normalise neural responses via divisive suppression, i.e. by dividing the stimulus drive by the activity of a pool of surrounding neurons (see Herrmann et al. [2010], and Cutrone et al. [2014] for empirical support; Beuth and Hamker [2015] for a mechanistic microcircuit model; and Wu [2017] for a philosophical summary of the alternative interpretation). Normalisation via divisive suppression is a canonical computation in the cortex that applies the same operations in a variety of contexts, and, depending on the context, is responsible for a large number of (attention-independent) effects from contrast normalisation, through cross-orientation suppression and surround suppression, to even object recognition (Carandini and Heeger [2012]).

 That is, according to the picture suggested by the findings reviewed in the previous section and also supported by the Normalisation Model of Attention, increased firing rate and receptive field reduction are not direct manifestations of the allocation of attention; they are only different consequences of attention-independent mechanisms (canonical computations) triggered by attention. Put it in another way, increasing the strength of neural responses and reducing receptive fields are not part of the core neural implementation of the allocation of attention—they are purely causal consequences of the fact that the neural processes that really implement the allocation of attention are in operation.

 The core neural realiser of the allocation of attention is the modulation of the local[[3]](#footnote-4) input of the built-in mechanisms in questions: attention multiplies or amplifies the presynaptic signals that provide the stimulus-specific inputs of the canonical neural computations of normalisation. We have seen that the amplification of these presynaptic signals is not attention specific: change in the contrast of the stimulus can evoke similar amplification. If, however, relevant stimulus-features are held fixed, then any amplification of these presynaptic signals is a sign of the allocation of attention. In this sense, then, the core neural realiser of attention is the not-stimulus-triggered amplification of the presynaptic signals providing stimulus-specific inputs of the built-in canonical neural computations of normalisation. This is what we call the Amplification View of attention.[[4]](#footnote-5)

 Before moving on, it is important to emphasise the difference between the Amplification View and the amplifier metaphor of the attention literature that often talks about attention as an amplifier (Fries et al. [2001], p. 1560) or booster (Wu [2014], p. 67). The standard usage of these terms exclusively refers to the gain mechanism, i.e. attention’s ability to increase firing rate—that is, a neuron’s output,—and thus is perfectly compatible with the claim that there is no single mechanism unifying attentional phenomena at the neural level.

 Contrary to this, the Amplification View offers a unificatory framework for thinking about the neural effects of attention. According to this view, the so-called modulatory effects of attention are really only effects—causal consequences that come about as a result of an interaction between the core realiser of attention (i.e. specific input signal amplification) and certain built-in mechanisms of perceptual processing. In some cases, this interaction results in boosting the strength of the neuron’s output, but in other cases it results in weakening it (as, for example, in the case of receptive field reduction when the non-preferred stimulus is attended). But even if the effects of the interaction of the allocation of attention with built-in mechanisms are diverse, the allocation of attention always consists in the amplification of the local input of these built-in mechanisms.

4 The Amplification View as an Account of Attention

This section discusses how the Amplification View is able to answer both the Disunity and the Overgeneralisation problems, and provide a full-fledged sub-personal level account of attention.

4.1 Answering the Disunity Problem

To see that the Amplification View is able to provide the unificatory framework promised in Section 3.2 consider the successes of the Normalisation Model in modelling the different neural effects of attention that previously couldn’t be accounted for in terms of a single explanatory scheme.

 The Normalisation Model of Attention offers a way to reconcile different conclusions regarding whether attention simply scales firing rates or sharpens tuning curves. The predictions of the model depend on the attentional strategy that is used to perform a given task. In the model a purely spatial attention strategy corresponds to an attention field that is constant across feature dimensions (orientation, direction of motion, etc.) but amplificatory for a specific spatial position. Under these conditions the model reproduces the multiplicative scaling of tuning curves. A purely feature-based attention strategy corresponds to an attention field that is amplificatory for a specific feature but not for spatial position. With such parameters the model is able to reproduce how feature-based attention sharpens the tuning curve. The model is also able to reproduce—in a similarly straightforward fashion—how the turning curve is modulated during receptive field remapping when there are two stimuli present in the receptive field: whereas attending the non-preferred stimulus reduces, attending the preferred stimulus increases the neural response (Reynolds and Heeger [2009]; Herrmann et al. [2010]; Herrmann et al. [2012]).

 The Normalisation Model is also able to reproduce the various forms of attentional modulation of the contrast-response function (contrast gain, response gain and mixed findings), depending on the stimulus conditions and the spread of the attentional feedback in the model. The relevant parameters are the stimulus size and the size of the attention field, relative to the sizes of the stimulation (the range of spatial positions and feature values that can evoke an excitatory response from the simulated neuron) and the suppressive fields (the range of spatial positions and feature values that can suppress the response of the simulated neuron). Depending whether these parameters are large or small, the Normalisation Model can reproduce all observed varieties of the gain mechanism. When the stimulus size is small and the attention field is large, then the model exhibits contrast gain (Reynolds et al. [2000]). When the stimulus size is large and the attention field is small, the model exhibits response gain. When the size of the stimulus and the size of the attention field are roughly equal in size to the stimulation field, the model predicts a gain intermediate between contrast and response gains (Williford and Maunsell [2006]). Note that these parameter-choices are not ad hoc—they match the characteristics (regarding the size of the stimulus field relative to the receptive field and the attentional strategies) of the specific experimental conditions under which the simulated effects were originally observed. (Reynolds and Heeger [2009], pp. 173-175)

 Over and above excitatory effects, the Normalisation Model can also reproduce inhibitory effects of attention, and can account for the ‘Mexican hat’ style response profiles of affected populations of neurons. To see how, recall that divisive normalisation normalises a neuron’s response by dividing its input by the activity of a surrounding pool of neurons. When attention targets a specific feature value (or spatial position) and consequently amplifies the input (and thus, under the right circumstances, enhances the output) of the neurons most sensitive to the specific feature value, it increases this divisive effect for neurons most sensitive to values close to the targeted one, since neurons that are most sensitive to values close to the targeted one will have the neurons with enhanced responses in their normalisation pool. Consequently, their output, which is also determined by divisive normalisation, will be negatively affected due to the higher denominator. Thereby, the activity of neurons whose normalisation pool includes neurons processing attended features will be suppressed.

 Normalisation mechanisms also play a crucial role in modulating response (spike-count) correlation between pairs of neurons. As Verhoef and Maunsell ([2017]) have very recently reported, normalisation mechanisms can shape response correlations through suppressive activity affecting the responses of populations of neurons. Depending on whether the neurons in question have similar or opposite stimulus preferences, the suppressive influences can be shared or antagonistic creating increasing or decreasing response correlations. Verhoef and Maunsell argue that attention capitalises on this built-in mechanism, and by amplifying the input of normalisation mechanisms indirectly increases or decreases the response correlation depending on whether it is allocated to non-preferred or preferred stimuli (respectively). That is, the Normalisation Model reproduces observed attentional effects of response correlation modulation as well.

 Finally, note that normalisation is a canonical computation that underlies a wide range of neural response properties throughout the cortex. Depending on the context, it is responsible even for effects like multi sensory integration (Ohshiro et al. [2011]), and object recognition (Carandini and Heeger [2012]). So the very same core realiser of attention that amplifies the input of normalisation mechanisms might very well underlie even the high-level effects that the allocation of attention has on, say, object perception.

 That is, the Amplification View—that identifies the core realiser of attention as the not-stimulus-triggered amplification of the presynaptic signals providing stimulus-specific inputs of normalisation mechanisms—is able to provide the unificatory framework that makes the Disunity Problem obsolete.

4.2 Answering the Overgeneralisation Problem

From the perspective of the Overgeneralisation Problem the Amplification View of Attention needs to be able to show that the specific neural mechanism that is claimed to be the core realiser of attention is not in operation in the absence of attention.

 The Amplification View claims that amplifying presynaptic signals of normalisation mechanisms is the core neural signature of attention. However, it seems that there are cases described in the neuroscience literature that involve similar processes but are entirely attention-independent, like the cellular mechanisms responsible for classical conditioning (Hawkins et al. [1983]), or the neural computations in the retina that distinguish local light intensity from global (Carandini and Heeger [2012]).[[5]](#footnote-6)

 On closer reflection, however, it is clear that such cases do not threat the Amplification View with overgeneralisation, since what they describe is not presynaptic signal amplification of a normalisation mechanism. Take the case of classical conditioning first. In their landmark paper Hawkins et al. propose that the cellular mechanism responsible for classical condition (in Aplysia) is ‘activity-dependent amplification of presynaptic facilitation’. Despite the similarity in the terms used, this mechanism is very different from the one the Amplification View identifies as the core realiser of attention. The mechanism behind classical conditioning is claimed to be the amplification of the ‘facilitation effect’ (that afferent facilitator connections can have on a neuron’s behaviour) by the synchronous firing of further neurons also providing afferent connections. Here the presynaptic signals involved are not amplified (only their facilitatory effect is enhanced), nor do they serve as inputs of a normalisation mechanism.

 In the case of retinal computation of local light intensity a normalisation mechanism is undoubtedly involved: retinal neurons are able to compute local values of light intensity and contrast exactly because local measurements are normalised by the mean of the measurements of a pool of surrounding cells (Carandini and Heeger [2012]). Nevertheless, no stimulus-independent amplification of presynaptic signal occurs, so it does not qualify as a (core) realiser of attention.

 At a more general level, the Overgeneralisation Problem claims that sub-personal accounts of attention commit a so-called mereological fallacy (Drayson [2012], [2014]) by ascribing the predicate of being attentive to collections of neurons, whereas only whole organisms can be correctly described as being attentive.

 There is something fundamentally insightful in the idea of mereological fallacy. The term ‘attention’ is part of the vocabulary of psychology, but it is certainly not part of the vocabulary of neuroscience. Neurons in themselves do not attend (see Wu [2014], p. 13). But the Amplification View is not guilty of the mereological fallacy. The Amplification View claims that the local input amplification of specific neural computations is the core realiser of attention. A core realiser is not sufficient for bringing about the phenomenon it realises—only a total realiser is (Shoemaker [1981]). Put it in another way: a personal level ascription of attention refers to a phenomenon that is a product of a rather complex neural mechanism. Neurons are constituent parts of the mechanisms that are responsible for organism level, i.e. psychological, functions like remembering, perceiving, or, for that matter, attending (see Machamer et al. [2000]; Craver [2007]). None of the individual parts of a mechanism does what the mechanism as a whole does (claiming otherwise would, indeed, be a mereological fallacy). Nevertheless, it is the organised activity of those very parts that is responsible for the overall behaviour (see Fazekas and Kertész [2011]). That is, it is not the amplification of the input of certain neural computations per se, but rather the activity of a much broader mechanism these neural computations are parts of in the normally functioning brain that is responsible for the personal level phenomenon of attending. On different occasions of personal level ascription of attention (for example when one looking for a friend attends to red T-shirts, or when one’s attention is drawn by a flashing light, etc.) the complex neural mechanisms producing the actual phenomenon might very well be different. However, the many different complex mechanisms all share a common part, namely the input amplification of specific neural computations. This is what unifies attentional phenomena at the neural level; this is what implements the allocation of attention in the brain.[[6]](#footnote-7) Any sub-personal account of attention (or any mental activity) should be interpreted in this way.[[7]](#footnote-8)

 However, it very well might be the case, or so the opponent’s argument goes, that sometimes when certain input signals of specific neural computations get amplified no sign of attention can be detected at the personal level. This would, again, be a case of overgeneralisation; the sub-personal level criterion is met, nevertheless, the system is allegedly non-attentive.

 Note that to reach such a conclusion one needs to be able to decide whether attention is present at the personal level. On what grounds can one make the relevant decision? It might be the case that a subject both reports lack of voluntary attending on his or her part and denies that his or her attention would be captured in a bottom-up manner. However, there is a near consensus these days that unconscious attention is possible (see Jiang et al. [2006]; Kentridge et al. [2008]; Kentridge [2011]; Norman et al. [2013]; for an overview see Wu [2014], pp. 112-114). That is, attentional capture might very well occur unconsciously, without any imprint in the subject’s stream of consciousness, and thus could very well remain out of reach for introspection. Subjective reports, thus, seem to be unreliable guides to attributing attention at the personal level.

 Organism level behavioural measures (for instance performance in discrimination tasks) are also often used to determine whether attention is in operation. When neuroscientists claim that certain neural activity corresponds to attention they typically reach such a conclusion on the basis of the detection of the particular neural activity in question in the context of subjects producing specific behavioural signs of attention (for reviews see Carrasco [2011] and Treue [2014]). Given all this, one could try to run the overgeneralisation argument in the following way: it seems very much plausible that there are cases where certain inputs of specific neural computations are amplified without there being any behavioural signs at the organism level, i.e. without the subject producing the specific behavioural signs that could indicate that attention is in operation.

 To answer this final challenge, recall that an organism level behaviour is the product of a complex sub-personal level mechanism (the total realiser). Input signal amplification is certainly only a tiny, although important, part of it (core realiser). No matter how important it is, though, without the activity of other constituents, and the right sort of organisation of such activities, the mechanism as a whole would not function properly, and thus would not be able to produce the right sort of behavioural outputs.[[8]](#footnote-9) So, of course, input signal amplification can occur without personal level behavioural signs. But it is perfectly compatible with the claim that input signal amplification is the core realiser of attention.[[9]](#footnote-10)

 The Amplification View, thus, is a promising sub-personal level approach that provides a unificatory framework for attentional phenomena at the neural level and is also able to avoid overgeneralisation, and hence it is a full-fledged account that has the potential to reframe our thinking about attention.

5 Attention as Selection vs. Attention as Amplification

In contemporary (at least scientific) literature, the fundamental function of attention is claimed to be selection. The Amplification View, however, suggests an entirely different picture according to which what is selective is not attention but those built-in perceptual mechanisms that attention interacts with. Attention itself it not selective, its fundamental function is amplification.

5.1 The Selection View

Reference to selection occurs at every level of description in scientific and philosophical theorising about the nature of attention. At the level of single neurons, for example, neuroscientists typically think of attention in terms of selection between stimuli competing for the same neural receptive field (see Desimone and Duncan [1995]). At the level where the perceptual hierarchy as a whole is the subject of interest psychologists famously identify attention with selection between information processing channels (see Broadbent [1958]; Deutch and Deutch [1963]; Lavie and Tsal [1994]). At the level of the whole organism philosophers often emphasise the importance of attention-as-selection in the control of behaviour and action initiation (see Wu [2011a], [2011b], [2014]).

 The idea that attention is essentially selection drove people to compare the functioning of attention with how filters (Broadbent [1958]; Treisman [1964], [1969]) and spotlights (Posner [1980]; Logan [1996]) work, thereby creating those fundamental metaphors that have been highly influential in the field.[[10]](#footnote-11) Originally, filtering mechanisms were thought of as providing a single bottleneck in information processing dividing it into a pre- and a post-attentive stage (Broadbent [1958]; Deutch and Deutch [1963]). However, nowadays there is a consensus that filtering effects occur throughout the processing stream (Driver [2001]) making it, at least, prima facie unclear what attention selects for. Accordingly, the Selection View is a heterogeneous position: some emphasise selection effects occurring early in the perceptual hierarchy and claim that attention selects for later stages of perceptual processing (Broadbent [1958]; Lavie [1995], [2005]); others emphasise selection effects occurring later in the processing stream and claim that attention selects for working memory processing (Deutsch and Deutsch [1963]; Knudsen [2007]; Prinz [2000], [2012]), or for global control (Rensink [2014]); still others emphasise selection effects linking perceptual stimuli to possible behavioural outputs and claim that attention is selection for action (Allport [1987], Neumann [1987], Wu [2011a], [2011b], [2014]).

 What serves as a common denominator of these different views is the idea that attention is fundamentally selective—that its essence manifests itself in the act of selection. That is, according to the Selection View, we attend to select, to control (that is, to restrict) the flow of information, to process only a particular stimulus by focusing on it and filtering out (or attenuating) competing stimuli. This is the view that we think the Amplification View can offer a viable alternative to.

5.2 The Amplification View as an alternative to the Selection View

The unificatory account provided by the Amplification View incorporates the selective effects of attention as well. Receptive field reduction, increased neural response to some stimulus feature combined with decreased neural response to other stimulus features, and suppressive effects around attended locations are all different neural underpinnings of attention’s acclaimed selectivity—and as we have seen, the Amplification View is able to account for all of these phenomena (see Sections 3.2 and 4.1).

 Note, however, that these neural implementations of selection are not direct effects of attention, but rather the outputs of the normalisation mechanism itself. It is the neural computation of normalisation that has this characteristic: it favours certain stimuli and can disregard others. As Carandini and Heeger put it, normalisation ‘exhibit[s] winner-take-all competition’ (Carandini and Heeger [2012], p.57). Recall how normalisation results in increased firing rate, receptive field reduction, surround suppression and response correlation purely driven by stimulus features like the contrast strength of the stimuli (see Sections 3.1, 3.2, 4.1). That is, normalisation, which is a canonical computation, a built-in perceptual mechanism, produces the selective effects—entirely independent of attention.

 Attention only interacts with the normalisation mechanism by amplifying its input corresponding to certain stimuli. Its role is purely amplificatory; it increases the stimulus-specific presynaptic signal that feeds into normalisation, which then, depending on the circumstances (see Section 4.1) can result in the selection of the corresponding stimulus. But not necessarily. Importantly, selection is not a necessary consequence of the interaction of attention and normalisation. In some cases, the effects of attention are not accompanied by selection in any sense. Take, for instance, the attentional effect on contrast perception in which attention increases perceived contrast such that a 22% contrast patch looks like an unattended 28% contrast patch (Carrasco et al. [2004]), or the attentional effect on perceived gap size in which attention makes a 0.20° gap look like an unattended 0.23° gap (Gobbell and Carrasco [2005]).[[11]](#footnote-12) As Block summarises these cases: ‘There are many convincing examples of attention changing appearance in a way that does not involve selecting some properties and de-selecting others’ (Block [2010], p. 31).

 The consequence is that according to the Amplification View, selectivity is not really a feature of attention itself, but rather a feature of the specific, built-in perceptual computations that attention is able to affect via its amplificatory role. This perceptual selection works without any contribution from attention. That is, according to the Amplification View, perception itself is selective, and attention only triggers these selective mechanisms—in certain, but not necessarily all, cases.[[12]](#footnote-13)

 This is a crucial departure from the Selection View. Under the Amplification View, attention is not just no longer essentially selective, it is not selective at all—its apparent selectivity is just a by-product of the fact that it triggers such built-in perceptual mechanisms, which themselves are selective.[[13]](#footnote-14)

5.3 Selective amplification

Before concluding the paper let’s first briefly consider a possible objection. One might argue that even if attention exerts its effects by amplifying certain input signals of built-in neural mechanisms, it does so only selectively: attention affects only some neural signals, namely those that correspond to the attended features or objects. That is, or so the objection goes, attention, even if it is realised by amplification, is essentially selective, since it core realiser amplifies only selected input signals.

 However, it is hard to see why such selective allocation would render attention itself selective. What is selective, rather, is the control mechanism that is responsible for the allocation of attention. Consider how a magnifying glass can be used in quite different ways: either by holding it close to one’s eye, more like spectacles, or by holding it close to the objects one wants to take a good look at. The latter use is highly selective compared to the former one: only a select few items can be magnified at once by the loupe. A magnifying glass itself, however, is not selective—what can be selective is the way it is used. Analogously, not attention, but only control mechanisms directing it to specific targets can be selective in this sense.

 In terms of controlling mechanisms, the literature distinguishes two different kinds of attention: bottom-up and top-down (Chun et al. [2011]; Carrasco [2011]). Whereas in the top-down case the subject initiates and directs the allocation of attention, bottom-up attention is a stimulus driven process that can automatically be captured independently of one’s volition. Crucial in the control of allocating attention is the so-called orienting network that prioritises sensory input (Posner and Petersen [1990]; Petersen and Posner [2012]; Diamond [2013]). It consists of two partly overlapping networks that can be corresponded to top-down and bottom-up orienting. The activity of the so-called dorsal frontoparietal network (including the intraparietal sulcus and the frontal eye field) influences perceptual processing in accordance with actual task demands, and is responsible for goal-directed stimulus-response selection. The other, more lateralised, so-called ventral frontoparietal network (including the temporoparietal junction and the ventral frontal cortex) plays a circuit-breaking role by breaking ongoing cognitive activity when a salient unexpected stimulus is detected. The dorsal system is associated with orienting top-down attention, whereas the ventral system is associated with orienting bottom-up attention (Corbetta and Shulman [2002]; Petersen and Posner [2012]; Wu [2014]).

 So what is traditionally labelled as ‘attention’ is, in fact, (at least) a two step process. The first step is allocating attentional resources in a particular way. This first step is controlled by the orienting network, and is often selective: it can target stimuli at a specific spatial location, or a particular stimulus-feature, or a whole object, etc. (Note, however, that even the allocation of attention is not necessarily selective, as it is the case with distributed attention.) This allocation determines the inputs of which normalisation mechanisms will be affected by attention—those that generate neural representations of the targeted stimuli. This interaction with the neural computations generating the representations of the targeted stimuli is the second step. The first step is how attention is allocated, the second step is how attention operates. How attention operates, i.e. the interaction between attention and the normalisation mechanisms, can result in a great variety of ways in which neural representations can be affected, many of which are traditionally characterised as selective effects. However, as we claim, there is nothing selective about how attention operates. Attention plays a uniform role of amplifying in a not stimulus driven way the presynaptic signals that provide stimulus-specific inputs of the normalisation mechanisms in question.[[14]](#footnote-15)

 Wayne Wu ([2017]) uses the divisive normalisation model to support his ‘selection for action’ view, which is a version of the Selection View. Wu interprets divisive normalisation as a process the output of which is to be identified with attention. In our view, attention is not the output of divisive normalisation. Instead, divisive normalisation is computed by an attention-independent built-in mechanism that produces its outputs even if attention is not in operation. Attention’s contribution is restricted to modulating these outputs by amplifying the input of the computation.

One might worry here that if according to the Amplification View the core realiser of attention is the not stimulus driven amplification of specific signals, then this definition will exclude instances of bottom-up attention, since bottom-up attention is driven by the salience of the stimulus, and thus is a stimulus-triggered phenomenon. Note, however, that what is stimulus driven in the case of bottom-up attention is the first step, the orientation, or allocation of attention. The first step in the case of bottom-up attention consists in the attention-independent perceptual processing of an unattended salient stimulus, which, then, due to the high salience of the stimulus in question, activates the circuit-breaking function of the control mechanism and triggers the re-allocation of attention to the salient stimulus. Once attention is allocated to this stimulus, it functions in accordance with the Amplification View amplifying the presynaptic signal (corresponding to the stimulus in question) providing an input for a normalisation mechanism. The stimulus attention is allocated to during the bottom-up capture of attention, thus, is already selected by built-in perceptual mechanisms (first step) before attention could start operating on it (second step). Thus the neural implementation of the second step does involve the not-stimulus-triggered amplification of the presynaptic signal corresponding to the stimulus in question even in the case of bottom-up attention as well, and hence it fits into the framework of the Amplification View neatly.

6 Conclusion

What is attention? The Amplification View offers a set of novel answers to this question. Contrary to the claim of the most influential theoretical framework (the biased competition model, see Desimone and Duncan [1995]), attention does not emerge from built-in perceptual processes (see also Wu [2017]), but it is an additional activity that interacts with these built-in perceptual mechanisms by amplifying some of their input signals. Contrary to contemporary philosophical consensus (see Wu [2014]; Watzl [2017]), attentional phenomena can be unified at the neural (sub-personal) level: the core realiser of attention is the not-stimulus-triggered amplification of the presynaptic signals providing stimulus-specific inputs for the built-in canonical neural computations of normalisation. And contrary to the received view at least in the scientific literature (see Carrasco [2011]; Petersen and Posner [2012]), the function of attention is not selection but amplification—while selection is achieved by built-in perceptual mechanisms, attention amplifies their afferent neural signals corresponding to attended stimuli. In the Marrian sense of how different levels of enquiry can inform each other (Marr [1982]), and also in the theory coevolution sense of how scientific explanations at different levels co-evolve (Churchland [1986]; McCauley and Bechtel [2001]), what we learn about the neural level informs how we think about the phenomenon at the psychological level. In accordance with this, the Amplification View sheds new light on the nature of attention by inviting us to think about the psychological function of attention differently—not as selection, but as amplification. The additional fact that while there are purely amplificatory effects that cannot be accounted for within the Selection View (see Section 5.2) selective effects can be accounted for within the Amplification View (see Section 3.2, 4.1, 5.2) renders the general framework that the Amplification View offers for thinking about the function of attention clearly superior to the traditional framework of the Selection View.

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*Peter Fazekas*

*Centre for Philosophical Psychology*

*University of Antwerp*

*Antwerp, Belgium*

*fazekas.peter@gmail.com*

*Bence Nanay*

*Centre for Philosophical Psychology*

*University of Antwerp*

*Antwerp, Belgium*

*bence.nanay@uantwerpen.be*

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1. Besides early visual processing, modulatory effects are just as common at higher levels of the visual stream (Noudoost et al. [2010]), and in post-perceptual mechanisms (Gazzaley and Nobre [2012]; Squire et al. [2013]), and also in non-visual modalities (Zelano et al. [2005], and Rinne et al. [2007]). [↑](#footnote-ref-2)
2. Other major models currently on the table are: the biased competition model (Reynolds et al. [1999]), the neurodynamical model (Rolls and Deco [2002]), the feedback model (Spratling and Johnson [2004]), the reentry hypothesis (Hamker [2005]), the feature similarity gain model (Martinez-Trujillo and Treue [2004]; Boynton [2005]), the cortical microcircuit model (Buia and Tiesinga [2008]), the integrated microcircuit model (Ardid et al. [2007]), and the selective tuning model (Rothenstein and Tsotsos [2014]). [↑](#footnote-ref-3)
3. The global input of perception, i.e. the stimulus induced signal generated by the transducers remains the same. [↑](#footnote-ref-4)
4. Note that this characterisation of the core realiser of attention as the not-stimulus-triggered amplification of the presynaptic signals providing stimulus-specific inputs of normalisation mechanisms is uniformly applicable to both lower- and higher-level perceptual processing. When attention targets higher-level representations, like, for instance, face-representations, as in the case of looking for a particular person in a crowded room, then attention amplifies those inputs of the neural computation normalising the responses of a specific population of neurons in the fusiform face area that correspond to relevant features of the particular face. Such amplified signals could have been the result of, say, a more salient object (with the specific properties) in the environment scanned. But that is not the case when attention is in operation. Attention mimics local manifestations of changing stimulus feature values, without actual physical changes happening in the environment. [↑](#footnote-ref-5)
5. Thanks for an anonymous referee for raising this objection. [↑](#footnote-ref-6)
6. A point of clarification. We argue from empirical results, so this is a claim about the realiser in humans and animal models used to study attentional phenomena. Our reductive account, thus, is reductive only in a local sense (Kim [1992]), and is compatible with the theoretical possibility of other creatures that produce behavioural signs of attention but have no nervous system at all. However, in agreement with Bechtel and Mundale ([1999]), we do think that multiple realisability based scepticism with regard to the role neuroscience can play in understanding cognition is misguided. In fact, the core-total realiser distinction helps appreciate why our kind of reductive explanation is compatible with multiple realisability in general. The total realiser, i.e. the whole mechanism the core realiser fits into to produce the behavioural signs of attention can be different for different behaviours, for similar behaviour in different species, for the same behaviour but in different individuals, even for the same behaviour in the same individual at different times. Yet, the core realiser is shared by all these different total realisers, and as such it provides a reductive explanation of attentional phenomena as it is able to specify a common underlying cause that, under different circumstances (as being a part of different total realiser mechanisms) brings about a vast number of different ‘effects of attention’. [↑](#footnote-ref-7)
7. Therefore, objections along the lines that attention cannot be identified with a neural amplificatory role because this type of signal enhancement can be implemented in clearly non-attentive systems (as for example musical amplifiers; Wu [2014], p. 69) attack a straw-man, since they disregard both (1) the fact that the Amplification View defines the core realiser of attention in terms of the amplification of the presynaptic signal providing the input of a normalisation mechanism, and (2) the fact that this definition is supposed to capture only the core realiser of attention. [↑](#footnote-ref-8)
8. Consider, for example, that an organism might very well be attending without any organism-level behaviour signs of attention, because, say, motor neurons are not functioning properly. [↑](#footnote-ref-9)
9. There is another version of the Overgeneralisation Problem, which clearly does not apply in the case of the Amplification View. It would go like this: if my vision is not perfect, then putting on glasses also has an amplificatory effect. But putting on glasses is blatantly not attention (see, for example, Watzl [2011]; Wu [2014], Section 4.4; Ganson and Bronner [2013] for versions of this argument). This objection misses the mark: according to our account, attention plays a very specific role by amplifying the input of certain built-in mechanisms in the nervous system, so that whereas the sensory stimulation is fixed, these build-in mechanisms respond as if the sensory stimulation wasn’t fixed. Putting on glasses does not effect specific built-in mechanisms in this particular way—it simply modulates the sensory stimulation itself. [↑](#footnote-ref-10)
10. The so-called biased competition model (Desimone and Duncan [1995]) that provided a functional description of how attention as a filter could work by advocating the importance of inhibitory mechanisms was originally pitched as an alternative to the spotlight-metaphor, i.e. the view that attention facilitates or enhances the processing of certain information (see Desimone and Duncan [1995], p. 194). However, nowadays, under the umbrella of the Selection View, the guiding metaphors of these historically different approaches are typically seen as synonymous with each other. A related metaphor that can be interpreted as an early departure from the Selection View is provided by the so-called zoom-lens model of attention proposed by Eriksen and St. James ([1986]). [↑](#footnote-ref-11)
11. In general, in this family of effects the allocation of attention shifts the percept of different prothetic stimulus features (that have a meaningful zero value and directionality) towards higher values along their characteristic dimension. For other examples see how attended stimuli appear to be more saturated (Fuller and Carrasco [2006]), and faster (Fuller et al. [2009]). [↑](#footnote-ref-12)
12. This consequence of the Amplification View is nicely in line with a popular high-level account of attention, the so-called Load Theory, that derives selective effects of attention from the inherently selective nature of perceptual processing itself (Lavie and Tsal [1994]; Lavie [1995], [2005]; Lavie and Dalton [2014]). [↑](#footnote-ref-13)
13. Jennings ([2012]) and Watzl ([2017]) in their own accounts of attention emphasise the function of prioritisation. Under the Amplification View prioritisation is also a result of built-in normalisation mechanisms (see also Serences and Kastner [2014]). Priority structures (Watzl [2017]) are determined by physical features and the operations of normalisation mechanisms even without attention. Attention affects priority structures only inasmuch as it interacts with the operations of the built-in perceptual mechanisms. [↑](#footnote-ref-14)
14. Note that the original Reynolds and Heeger ([2009]) Normalisation Model of Attention that we rely on to motivate the Amplification View (Sec. 3.2) captures these two steps via two parameters of the so-called attention field that gets multiplied by the stimulus drive point-by-point across the population of neurons. This attention field is 1 everywhere except a range of spatial positions and/or features values where it is greater than 1. The distribution of this attentional gain, i.e. the specific spatial positions and/or feature values where the attention field is greater than 1 captures the allocation of attention, whereas the specific value of the attentional gain in these positions (together with the feature of model that the attentional field gets multiplied by the stimulus drive) determines how attention interacts with the normalisation mechanism. The former is how the model simulates orienting, the latter is how the model simulates the operation of attention. [↑](#footnote-ref-15)