

The many characters of visual alpha oscillations

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Abstract

A central feature of human brain activity is the alpha rhythm: a 7–13 Hz oscillation observed most notably over occipitoparietal brain regions during periods of eyes-closed rest. Alpha oscillations covary with changes in visual processing and have been associated with a broad range of neurocognitive functions. In this article, we review these associations and suggest that alpha oscillations can be thought to exhibit at least five distinct ‘characters’: those of the inhibitor, perceiver, predictor, communicator and stabiliser. In short, while alpha oscillations are strongly associated with reductions in visual attention, they also appear to play important roles in regulating the timing and temporal resolution of perception. Furthermore, alpha oscillations are strongly associated with top-down control and may facilitate transmission of predictions to visual cortex. This is in addition to promoting communication between frontal and posterior brain regions more generally, as well as maintaining ongoing perceptual states. We discuss why alpha oscillations might associate with such a broad range of cognitive functions and suggest ways in which these diverse associations can be studied experimentally.

Introduction

Most features of electrical brain activity are difficult to identify in live recordings. The majority require statistical manipulations and averaging over many trials to be clearly distinguished from noise. Nevertheless, when people close their eyes, a clear and sustained oscillation reliably emerges from this background, with maximum amplitude over posterior brain regions and within a frequency range of approximately 7–13 Hz (Fig. 1A). These prominent rhythms are known as ‘alpha’ oscillations and have been a topic of interest for many: from researchers trying to measure concentration (Clayton *et al.*, 2015) to artists reporting intense visions during exposure to flickering lights at alpha frequencies (Ter Meulen *et al.*, 2009). Occurrence of these rhythms is widely accompanied by reductions in cognitive activity, supporting the view that they primarily reflect processes of attentional disengagement (Pfurtscheller *et al.*, 1996; Lundqvist *et al.*, 2013).

This association between alpha and task disengagement has strongly influenced the ways in which researchers explain changes in alpha amplitude (or ‘power’) that are observed across a broad range of studies (e.g. Jokisch & Jensen, 2007; Klimesch *et al.*, 2011; Mo *et al.*, 2013). In one representative example, although

alpha power has been both positively and negatively associated with sustained visual attention, suggested reasons for these contrasting effects have assumed a correspondence between alpha and reduced cortical processing in both cases (Dockree *et al.*, 2007; Clayton *et al.*, 2015). Nevertheless, recent studies have begun to question this view of alpha, suggesting a more nuanced perspective in which the roles of alpha rhythms in cognition are multifaceted. In addition to their association with reduced visual processing (Pfurtscheller *et al.*, 1996), alpha oscillations have been suggested to support many neurocognitive functions that are central to the engagement of visual attention (Sadaghiani & Kleinschmidt, 2016; Sherman *et al.*, 2016; Piantoni *et al.*, 2017). Such suggestions are broadly consistent with early ideas of researchers like Walter (1953) that, rather than existing as a singular phenomenon, alpha oscillations should be thought of as a ‘family’ of distinct, neural rhythms.

In this article, we review current evidence on the ways in which alpha oscillations covary with distinct aspects of visual processing. Specifically, after providing a brief account of how alpha oscillations are generated in the brain, we suggest that alpha contributes to visual processing by exhibiting at least five distinct ‘characters’: those of the inhibitor, perceiver, predictor, communicator and stabiliser. We hope that this article can highlight the diverse ways in which alpha oscillations may support visual cognition, and that it can facilitate interpretation of new findings in the field that might appear inconsistent with more established theories. Before continuing, it should be noted that, in addition to visual regions of the brain, alpha oscillations are observed in auditory (Leske *et al.*, 2014), sensorimotor (Haegens *et al.*, 2015) and prefrontal areas (Supp *et al.*, 2011), as well as the hippocampus (Schürmann *et al.*, 2000), and brain stem (Barman & Gebber, 2007). To avoid confusion, we focus exclusively in this article on alpha oscillations

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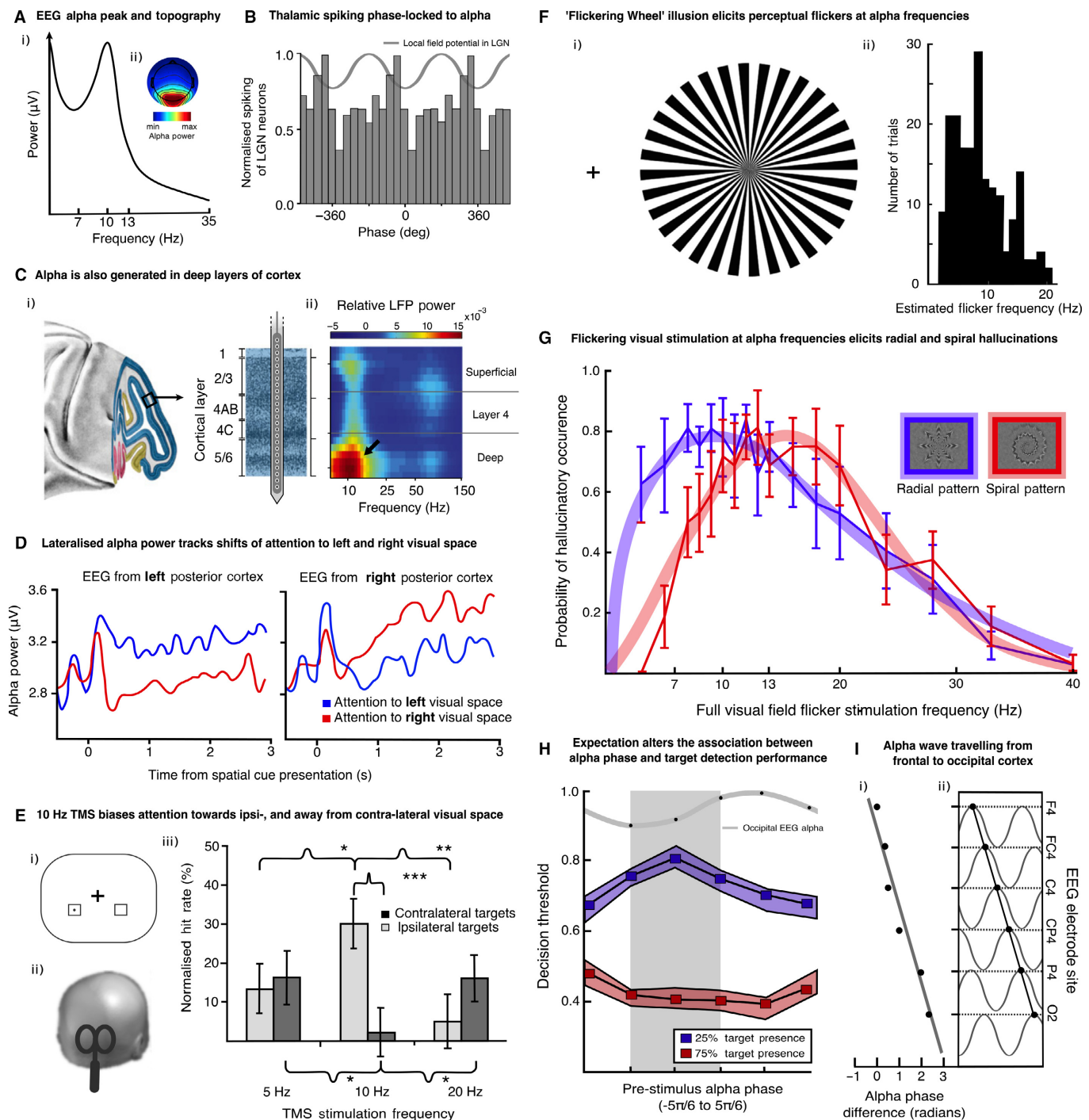
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recorded maximally over posterior brain regions or localised to occipitoparietal cortex. From this point onwards, the term 'alpha oscillations' will refer only to these posterior rhythms.

The generators of alpha

Oscillations can be generated by a diverse range of neurobiological mechanisms, from cyclical processes occurring in individual neurons, to network effects that are observed over larger spatial scales (Buzsáki, 2006; Wang, 2010). Furthermore, in addition to being expressed across many regions of the brain (e.g. Haegens *et al.*, 2015), alpha oscillations have been recorded in the firing patterns of

a range of neuronal cell types (Wang, 2010; Womelsdorf *et al.*, 2014). Such findings indicate that alpha oscillations are most likely generated by variety of neural processes. Nevertheless, existing evidence suggests that certain brain areas and neural circuit types are more likely than others to play significant roles in generating alpha rhythms.

For example, alpha oscillations have long been associated with activity in the thalamus (Berger, 1929). Support for this view comes from evidence that thalamic lesions profoundly diminish alpha oscillations (Ohmoto *et al.*, 1978; Lukashevich & Sazonova, 1995), and that changes in electroencephalographic (EEG) alpha power covary with haemodynamic activation in the thalamus (Goldman *et al.*,

FIG. 1. (A) EEG Alpha Peak and Topography. (i) An example of an EEG frequency-power spectrum recorded from electrode P3 during a visual attention task. This spectrum follows a negative exponential distribution with the exception of a Gaussian-shaped peak in the alpha band (7–13 Hz). (ii) When the spatial distribution of this alpha activity is calculated, it is commonly found to be greatest at posterior electrode sites (adapted from Helffrich *et al.*, 2014). (B) Thalamic spiking phase-locked to alpha. Normalised spike rates of thalamocortical neurons are displayed for the different phase positions of an ongoing alpha oscillation. This oscillation is observed in local field potentials recorded in the lateral geniculate nucleus (LGN; grey line). Subsets of thalamocortical neurons are shown to cluster their firing around the trough of the ongoing alpha oscillation. Note that other groups of thalamocortical neurons (not shown here) conversely exhibit maximum firing around the peak of ongoing alpha (adapted from Lőrincz *et al.*, 2009). (C) Alpha is also generated in deep layers of cortex. (i) A lateral view of the macaque brain. Regions highlighted in blue correspond to area V1. Multidepth electrodes implanted into this region enable recording of visual activity across all layers of cortex. (ii) A frequency-power spectrogram is shown across cortical layers. Relative power in the alpha band is greatest in deep vs. superficial layers (adapted from van Kerkoerle *et al.*, 2014). (D) Lateralised alpha power tracks shifts of attention to left and right visual space. Posterior EEG alpha power is shown following presentation of cue stimuli in a visuospatial attention task. These cue stimuli tell participants to shift their attention to either the left or right sides of visual space. This shifting of attention increases alpha power over posterior cortex ipsilateral to the attended hemifield (i.e. over areas of visual cortex that will not process the anticipated visual stimulus; adapted from Kelly *et al.*, 2006). (E) 10 Hz TMS biases attention towards ipsi- and away from contralateral visual space. (i) Participants were required to detect the presentation of faint black dots in either the left or right sides of visual space. (ii) TMS was applied at a range of frequencies to lateral visual cortex immediately preceding the presentation of these faint dots. (iii) TMS at 10 Hz improved detection performance when delivered to visual cortex ipsilateral to the presented stimuli, but impaired performance when delivered to contralateral visual cortex. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$ (adapted from Romei *et al.*, 2010). (F) ‘Flickering Wheel’ illusion elicits perceptual flickers at alpha frequencies. (i) When viewed in the visual periphery (e.g. when focusing on the left-hand fixation cross), these circular spokes are often perceived to flicker. (ii) A histogram showing the distribution of estimated frequencies of the perceived illusory flicker over many trials. Participants most commonly matched this illusory flicker to reference flickers in the alpha band. Note that, in the original dataset, the illusion was also matched to a flicker of around 45 Hz on one trial (adapted from Sokoliuk & VanRullen, 2013). (G) Flickering visual stimulation at alpha frequencies elicits radial and spiral hallucinations. The probability of the occurrence of spiral and radial hallucinatory patterns is plotted for visual flickers at different frequencies. Radial patterns (blue line) are more commonly reported at flicker frequencies just below 10 Hz, while spiral patterns (red line) are more commonly perceived at flicker frequencies just >10 Hz. In general, though, hallucinatory patterns are most commonly perceived at flicker frequencies in the alpha band (i.e. 7–13 Hz). Error bars display SEM across observers. Thick background lines represent the best-fitting Weibull function to the grand-average data (adapted from Mauro *et al.*, 2015). (H) Expectation alters the association between alpha phase and target detection performance. The relationship between decision threshold and binned occipital 10 Hz EEG phase 119 ms prior to stimulus presentations. Grey shading indicates the phase values that maximally predict the influence of expectation on decision. An intermediate phase position (approximately 0 degrees) was associated with a higher decision threshold in the expect 25% target presence condition, but a lower threshold in the expect 75% target presence condition. In other words, decisions were maximally biased towards reporting ‘no’ when participants did not expect a stimulus to be presented, but towards ‘yes’ when participants did expect a stimulus to be presented. Shaded, coloured outlines represent within-subject SEM (adapted from Sherman *et al.*, 2016). (I) Alpha wave travelling from frontal to occipital cortex. (i) An example of gradual phase shifts along a chain of electrodes from F4 to O2 for one subject. The black dots reflect the different phase difference values. The solid line shows a linear fit to these values (adapted from Patten *et al.*, 2012). (ii) An illustration of how these gradual phase shifts would appear in EEG recordings from F4 to O2.

2002; Liu *et al.*, 2012). Electrophysiological recordings also reveal strong coherence between alpha oscillations in visual cortex and the thalamus (Chatila *et al.*, 1992; Lőrincz *et al.*, 2009). Specifically, the phase of alpha has been found to correlate with the spiking activity of thalamocortical neurons in anterior layers of the lateral geniculate nucleus (Chatila *et al.*, 1992; Lőrincz *et al.*, 2009). These neurons are thought to facilitate transfer of visual information to cortex and cluster their spiking around the peaks and troughs of ongoing alpha oscillations (Fig. 1B). The rhythmicity of these thalamocortical neurons, and the phase position at which they fire, is strongly influenced by phasic inhibition from interneurons in the lateral geniculate nucleus (Lőrincz *et al.*, 2009). Alpha oscillations in both interneuron and thalamocortical activity in the lateral geniculate may also be coordinated by local circuits that are connected by gap junctions, producing sustained cycles of activity at alpha frequencies (Hughes *et al.*, 2011). Consequently, it seems that alpha oscillations are generated by a range of interconnected processes in the thalamus, and that these rhythms may be used to segment visual inputs into distinct subgroups (Lőrincz *et al.*, 2009). However, there is also evidence that alpha oscillations are generated in large part by cortical activity.

This point is shown by the finding that pyramidal neurons from deep layers of cortex exhibit rhythmic firing at alpha frequencies when isolated from the thalamus in *in vitro* preparations (Silva *et al.*, 1991). Furthermore, while laminar recordings of visual cortex *in vivo* have identified generators of alpha oscillations in all layers of cortex (Bollimunta *et al.*, 2008), greater alpha synchrony has often been observed in deep vs. superficial layers (Fig. 1C; Buffalo *et al.*, 2011; van Kerkoerle *et al.*, 2014; although see Haegens *et al.*, 2015). The hypothesis that cortex plays an independent role in alpha generation is also supported by the finding that alpha oscillations exhibit stronger coherence between cortical areas than they do between cortex and the thalamus (Da Silva *et al.*, 1973).

In particular, alpha power in diverse regions of posterior cortex has been found to correlate most significantly with the structural and functional connectivity of those regions with primary visual cortex (Hindriks *et al.*, 2015). Alpha may even represent an intrinsic rhythm of visual cortex given that transcranial magnetic stimulation of this region evokes oscillations mostly in the alpha band, whereas stimulation of more anterior regions evokes only higher frequency rhythms (Rosanova *et al.*, 2009). Consequently, although alpha oscillations are generated in large part by activity in the thalamus, they are also strongly influenced by activity in posterior cortical regions. Alpha oscillations therefore reflect a complex product of both thalamocortical and corticocortical interactions in visual cortex. It should therefore be unsurprising that alpha oscillations have been intimately linked with many functions of visual processing. We dedicate the following sections to discussing these associations.

The characters of alpha

Alpha the inhibitor

Increases in the amplitude of alpha oscillations have generally been associated with impairments in visual processing. Alpha power reduces rapidly in visual regions during periods of increased visual attention, but strengthens when these regions become disengaged (Fries *et al.*, 2008). This process is observed during shifts of spatial attention, in which reductions in alpha power are observed over the hemisphere processing attended visual space, whereas increases in alpha power are observed over the opposite hemisphere (Fig. 1D; Worden *et al.*, 2000; Kelly *et al.*, 2006; Gould *et al.*, 2011; Samaha *et al.*, 2016). Such differences in alpha power between the two visual hemispheres have been associated with improved detection of attended, lateral stimuli in recordings of both spontaneous

(Boncompagni *et al.*, 2016) and task-related brain activity (Gould *et al.*, 2011). Spontaneous reductions in alpha power have also been associated with increases in the excitability of visual cortex. For example, during spontaneous periods of low alpha power, people are more likely to report seeing visual phosphenes during transcranial magnetic stimulation of visual cortex (Romei *et al.*, 2008) and to perceive visual stimuli when none has been presented (Iemi *et al.*, 2017). Furthermore, supporting the negative association between alpha power and visual excitability, static magnetic field stimulation of visual cortex, which is thought to inhibit neural activity (Oliviero *et al.*, 2011), induces significant increases in alpha power (Gonzalez-Rosa *et al.*, 2015).

Alpha oscillations have therefore been suggested to reflect periods of visual inactivity (Pfurtscheller *et al.*, 1996; Lundqvist *et al.*, 2013). However, in addition to marking disengagement, alpha may also play active roles in suppressing visual activity. Strong evidence in support of this view comes from observations of increased alpha power when visual processing must be actively inhibited. For example, alpha power commonly increases when people are required to maintain information in visual working memory and therefore must prevent memorised information from being corrupted by irrelevant visual inputs (Jensen *et al.*, 2002; Jokisch & Jensen, 2007). When distracting images are presented during these periods of memory retention, increases in alpha power are found to predict reduced processing of task-irrelevant stimuli (Bonnefond & Jensen, 2012, 2013). Furthermore, in contrast to the aforementioned studies linking alpha primarily with visual disengagement (e.g. Iemi *et al.*, 2017), increases in alpha power during periods of memory retention are greatest with increased memory load (Jensen *et al.*, 2002; Tuladhar *et al.*, 2007). Such alpha increases are also associated with improved memory performance (Lozano-Soldevilla *et al.*, 2014).

Alpha oscillations may therefore represent an active mechanism of inhibition that serves to suppress irrelevant visual processing (Jensen & Mazaheri, 2010; Clayton *et al.*, 2015). Causal evidence to support this view is provided by the finding that transcranial magnetic stimulation of lateral visual cortex at 10 Hz, which is known to entrain alpha oscillations (Thut *et al.*, 2011), biases attention away from areas of visual space processed by the stimulated region. This is in contrast to stimulation at 5 and 20 Hz (Fig. 1E; Romei *et al.*, 2010). Alpha oscillations may suppress visual processing by directly activating inhibitory systems in the brain. This was suggested by van Kerkoerle *et al.* (2014) who proposed that alpha oscillations are driven in large part by the activity of layer 6 neurons in visual cortex, which are known to inhibit local processing by directly activating local inhibitory neurons (Olsen *et al.*, 2012). Of relevance to this point is the finding that optogenetic stimulation of layer 6 cortical neurons at 10 Hz inhibits sensory thalamus (Crandall *et al.*, 2015). Another explanation for the link between alpha and inhibition is that increases in alpha power reflect a transition towards neural hypersynchrony, which is known to impair sensory processing (Rajagovindan & Ding, 2011; Supp *et al.*, 2011). However, despite links between alpha oscillations and sensory suppression, it is important to note that these inhibitory effects of alpha are fundamentally rhythmic rather than tonic in nature. While sustained increases in alpha power may associate with sustained reductions of visual processing, such reductions are nevertheless applied in rhythmic cycles of approximately 100 ms (often referred to as 'pulsed inhibition'; Mathewson *et al.*, 2011). These cycles represent an intrinsic property of the inhibitory effects of alpha. However, they also appear to play important roles in facilitating visual perception.

Alpha the perceiver

A curious visual illusion was recently reported by Sokoliuk & VanRullen (2013) in which a stationary, radial image, composed of black and white spokes, appears to flicker at a rapid pace when viewed in the visual periphery. In a perceptual matching task, in which people were asked to compare this illusion to genuinely flickering stimuli, people reported the closest similarity to flickers at alpha frequencies (Fig. 1F). Furthermore, the intensity of this illusion correlated positively with EEG alpha power, with flickers most often reported during periods of high alpha power (Sokoliuk & VanRullen, 2013). This finding suggests that alpha oscillations, rather than universally inhibiting visual processing, may also facilitate periodic sampling of visual information from the environment. Consistent with this view, many studies have shown that visual stimuli are better processed when presented at the trough of an alpha oscillation compared to its peak (Busch *et al.*, 2009; Mathewson *et al.*, 2009; Dugué *et al.*, 2011). Furthermore, the amplitude of gamma oscillations (30–100 Hz) in visual cortex is known to covary with changes in alpha phase (Osipova *et al.*, 2008; Bahramisharif *et al.*, 2013). As gamma oscillations are strongly associated with stimulus processing (Fries *et al.*, 2008), this again suggests the involvement of alpha oscillations in the cyclical regulation of perception.

Such cycles may be used as a mechanism to regulate the timing of visual attention. For example, telling someone when an upcoming visual stimulus will be presented facilitates the perception of that stimulus and biases alpha phase towards the optimal position for visual processing (Samaha *et al.*, 2015). Alpha oscillations can also be reset by auditory stimuli, perhaps facilitating multisensory interactions to aid perception of external stimuli (Romei *et al.*, 2012). Furthermore, when people are shown flickering images at alpha frequencies, a process known to reset the phase of alpha oscillations (Spaak *et al.*, 2014; Notbohm *et al.*, 2016), subsequently presented visual stimuli are better detected when displayed in phase with that initial flicker (Mathewson *et al.*, 2012; Spaak *et al.*, 2014). This finding may reflect entrainment of visual attention at alpha frequencies to predictable, cyclical patterns in the environment (Mathewson *et al.*, 2010). Nevertheless, it should be noted that, in contrast to the findings of Samaha *et al.* (2015), expectations of stimulus presentations have been found to modulate alpha power while leaving alpha phase unaffected (van Diepen *et al.*, 2015).

In addition to influencing the timing of visual attention, alpha oscillations in posterior cortex may also regulate the temporal resolution of perception. For example, two visual flashes presented within one alpha cycle (i.e. ~100 ms) are often perceived as a single event (Kristofferson, 1967). People with a high alpha peak frequency are better able to correctly classify double flashes as separate events, indicating a positive relationship between the speed of an individual's alpha oscillations and the temporal resolution of their perception (Samaha & Postle, 2015). Furthermore, alpha peak frequencies have been found to increase, compared to periods of rest, when people perform challenging visual tasks that require greater processing of visual information (Haegens *et al.*, 2014). It therefore seems that alpha oscillations may play active roles in both segmenting visual inputs into discrete events and regulating the speeds of visual processing. On a related note, alpha oscillations have been suggested to play an important role in the 'triple flash' illusion: a phenomenon where people report seeing three visual stimuli when only two have been presented. This illusion occurs when the interval between stimulus presentations is ~100 ms. It has been theorised that the illusion may therefore be caused by a superposition of two

alpha oscillations, evoked by each of the two visual stimuli, that creates a third peak of activation when the delay between these evoked oscillations matches their oscillatory period (e.g. 100 ms; Bowen, 1989). Consistent with this idea, the optimal stimulus onset asynchrony for this illusion has been found to correlate with individual peak alpha frequency in parietal, but not occipital cortex (Gulbinaite *et al.*, 2017). This finding suggests that alpha oscillations can induce experiences of visual stimuli that have not been presented, further supporting the positive association between alpha and visual perception. The finding also highlights the point that alpha peak frequencies can differ between regions of posterior cortex (e.g. Haegens *et al.*, 2014), and suggests that alpha activity in parietal cortex may be more important for regulating visual perception than alpha in visual cortex.

In addition to these associations between alpha oscillations and cycles in visual perception, many other studies suggest associations between alpha and perception that go beyond rhythmic fluctuations. For example, although presentation of visual images with low spatial frequency increases gamma power in visual cortex, images with high spatial frequency evoke greater increases in the alpha band (Fründ *et al.*, 2007). Conscious perception of near-threshold visual stimuli has also been associated with increased alpha power in occipital and fronto-parietal regions (Babiloni *et al.*, 2006). Furthermore, many event-related components associated with visual perception have been suggested to reflect stimulus-induced resetting of alpha phase (e.g. P1; Makeig *et al.*, 2002; Fellerger *et al.*, 2011). This resetting increases the consistency of alpha phase following presentation of visual stimuli, meaning that alpha rhythms can be observed in averaged EEG data time-locked to those stimuli. Such 'evoked' oscillations contrast with 'induced' oscillations, which are defined as modulations of oscillatory power that are not consistently phase-locked to stimulus presentations (e.g. Tallon-Baudry & Bertrand, 1999; David *et al.*, 2006). On a separate note, further supporting the association between alpha and visual perception, presentation of flickering lights at alpha frequencies to individuals with their eyes closed has been found to induce a range of visual experiences: rings, squares and spirals of different colours and intensities (Shevelev *et al.*, 2000; Mauro *et al.*, 2015; Pearson *et al.*, 2016). These visions are altered by the frequency of the flicker, with individuals most commonly reporting radial images when stimulated at frequencies of <10 Hz, and spiral images when stimulated above 10 Hz (Fig. 1G; Mauro *et al.*, 2015). In general, though, such hallucinations are reported with the highest probabilities when flickering stimulation is delivered at an individual's peak alpha frequency (Kamenkovich *et al.*, 1997; Shevelev *et al.*, 2000). Furthermore, these experiences have been reported to vary with the direction in which alpha oscillations propagate through the brain, with ring and spiral hallucinations associated with alpha rhythms travelling from occipital to frontal cortex (Shevelev *et al.*, 2000). Consequently, while an extensive body of research links alpha oscillations to periodic regulation of visual perception, there is also evidence suggesting a positive association between alpha activity and the perception of complex visual images. One reason for this association might be the link between alpha oscillations and feedback signalling in visual cortex.

Alpha the predictor

Alpha oscillations are observed with different levels of synchrony across different cortical layers (although see Haegens *et al.*, 2015). Specifically, alpha oscillations are often recorded with higher amplitudes in deep layers of cortex, while gamma oscillations dominate

superficial layers (Buffalo *et al.*, 2011; van Kerkoerle *et al.*, 2014). Pyramidal neurons in superficial layers are thought to project in a bottom-up fashion to higher level regions, while deep layers exhibit feedback projections in the opposite direction (Felleman & Van Essen, 1991; Salin & Bullier, 1995; Sherman & Guillery, 1998). It has therefore been suggested that these different directions of travel in the brain may be distinguished by different frequencies of neural activity: with gamma oscillations reflecting bottom-up processing and alpha/low-beta oscillations communicating feedback (Bastos *et al.*, 2015; Jensen *et al.*, 2015). This idea was recently supported by Michalareas *et al.* (2016) who identified areas of visual cortex and classified their interactions as either feedback or feedforward using tractography data collected in macaques. Analysing magnetoencephalography in humans, Michalareas *et al.* (2016) found that Granger causality from high to low levels of visual cortex (i.e. feedback interactions) was strongest around an alpha peak of 11 Hz, whereas interactions in the opposite direction were predominantly in the gamma band (~60 Hz). This view that alpha facilitates feedback processes in the brain is also supported by the finding that electrical stimulation of area V4 in macaques elicits alpha oscillations in the lower area V1, whereas microstimulation of V1 elicits gamma oscillations in V4 (van Kerkoerle *et al.*, 2014). Interestingly, these electrically evoked alpha rhythms in V4 were suppressed when NMDA receptors were blocked. As NMDA is thought to be involved in feedback processing (Self *et al.*, 2012), this suggests a further interaction between alpha oscillations and the neurochemical mechanisms of top-down control. Of relevance to this point is the finding that a cholinergic agonist strengthens the lateralisation of alpha power in visual cortex when participants shift their attention to one side of visual space (Bauer *et al.*, 2012). Acetylcholine has also been implicated in feedback processing (e.g. Deco & Thiele, 2011).

While the strongest evidence linking alpha/low-beta oscillations to feedback comes from these kinds of physiological investigations, further evidence has also been provided by behavioural studies. For example, when individuals self-generate auditory or visual stimuli (e.g. press a button to display a stimulus), alpha power increases in areas of sensory cortex that process this self-generated information (Stenner *et al.*, 2014; Cao *et al.*, 2017). Although such increases in alpha power could reflect suppression of irrelevant sensory processing, these findings also suggest the possible involvement of alpha in communicating predictions to sensory cortex (Cao *et al.*, 2017). This idea has received support from the observation of increased pre-stimulus alpha power in task-relevant brain networks when participants are able to predict the identity of an upcoming stimulus (Mayer *et al.*, 2016). It is also interesting to note that top-down predictions about the likely timings of upcoming visual stimuli may be implemented by modulations of alpha phase (Samaha *et al.*, 2015). However, perhaps the strongest evidence to support the involvement of alpha oscillations in top-down prediction comes from a recent study by Sherman *et al.* (2016). Here, participants were required to detect the occurrence of briefly presented Gabor patches. On each task block, participants were told that these patches would be presented on either the minority or majority of trials. As with previous studies, an association was observed between target detection performance and alpha phase at the moment of stimulus presentation. However, participants' expectations had a significant effect on this association. Although participants were more likely to respond to a Gabor patch delivered at an intermediate phase position (0°) in blocks with majority target occurrence, this same phase position was conversely associated with a lower propensity to respond in blocks with minority target occurrence (Fig. 1H). In other words, a phase position between the peak and trough of the alpha oscillation was

associated with a more liberal response bias when targets were common, but a conservative bias when they were rare. Given that the trough of alpha has, in contrast, been associated with improved processing of external stimuli (e.g. Busch *et al.*, 2009), this suggests that alpha oscillations may reflect periods of alternation between bottom-up processing and top-down predictions in visual cortex.

Alpha the communicator

Extending this view that alpha facilitates transmission of predictions to visual cortex, alpha oscillations have been associated more widely with propagation of activity throughout the brain. This is particularly true of communication among occipital, parietal and frontal regions (Sadaghiani & Kleinschmidt, 2016), as well as between thalamus and posterior cortex (Saalmann *et al.*, 2012). A central way in which these oscillations could facilitate propagation of activity is by synchronising cycles of excitability between distant brain areas, and thereby increasing the likelihood that spikes from one area will arrive during the excitable phase of the other (Fries, 2005). Consistent with this idea, when individuals shift their attention to one side of visual space, alpha oscillations in both frontal and parietal cortex have been found to synchronise with alpha oscillations in visual cortex contralateral to the attended hemifield (Sauseng *et al.*, 2005; Doesburg *et al.*, 2009). This long-range synchronisation of alpha occurs simultaneously with local alpha synchronisation in ipsilateral visual cortex, suggesting the involvement of alpha in both sensory inhibition and integration of top-down control networks dedicated to the coordination of visual attention (Doesburg *et al.*, 2009). Alpha oscillations have also been reported to synchronise between frontal and parietal areas when individuals recognise visual objects (Freunberger *et al.*, 2008) and during retention of information in visual working memory (Doesburg *et al.*, 2010; Daume *et al.*, 2017). However, alpha oscillations may also facilitate long-range transmission of information by propagating across the brain in travelling waves.

Travelling alpha waves were reported in some of the earliest EEG studies (Hughes, 1995). In contrast to long-range synchronisation, in which phase differences are usually fixed between communicating regions (often with 0° phase lag; Fries, 2005), travelling waves are defined as periods in which phase differences between brain regions increase linearly with distance from a target region (Patten *et al.*, 2012). For example, an alpha wave travelling from frontal to posterior cortex would be observed as a gradual increase in the phase lag of alpha activity along a fronto-posterior axis with respect to a frontal lead electrode (Fig. 1I). Such travelling waves have been reported in a number of brain regions, and over a range of frequencies (e.g. Lubenov & Siapas, 2009). Nevertheless, alpha and gamma oscillations recorded at occipitoparietal electrode sites have been found to exhibit the most diverse and reliable phase differences with respect to activity recorded at other electrode sites (van Ede *et al.*, 2015). Given that alpha waves commonly travel at speeds of 5–15 m/s (Hughes, 1995), as measured by tracking the progression of alpha phase between electrode sites (e.g. Patten *et al.*, 2012), alpha waves have been argued to most likely reflect corticocortical propagation of activity (Hindriks *et al.*, 2014). However, given the known involvement of the pulvinar in synchronising visual regions at alpha frequencies (Saalmann *et al.*, 2012), travelling alpha waves may also be coordinated by the thalamus (Llinas *et al.*, 1998).

Travelling waves are thought to play important roles in visual processing (Han *et al.*, 2008; Muller *et al.*, 2014). Presentation of visual stimuli can generate travelling alpha waves that propagate from occipital to frontal cortex (Klimesch *et al.*, 2007; Patten *et al.*, 2012). As described before, the direction of such travelling waves

through the brain influences the nature of visual hallucinations caused by alpha-frequency flickers (Shevelev *et al.*, 2000). Furthermore, in an invasive recording study, Bahramisharif *et al.* (2013) found that gamma activity in visual cortex, known to play an important role in sensory processing, is coordinated by alpha oscillations that propagated across posterior cortex. Such alpha oscillations have also been found to travel from high- to low-level regions of cortex. For example, alpha oscillations in area V1 lag behind those of V4, with Granger causality analysis indicating a flow of alpha activity between these regions in a top-down manner (van Kerkoerle *et al.*, 2014). Furthermore, reaction times are reportedly faster to visual stimuli that are presented during the occurrence of alpha waves propagating from frontal to occipital cortex, compared to the opposite direction (Patten *et al.*, 2012). This finding again points to an association between alpha waves travelling along a fronto-posterior axis and the engagement of top-down control. Consequently, it seems that alpha oscillations can facilitate communication across the brain through multiple means: both via synchronisation of activity within functional brain networks, and through the direct propagation of activity through the brain.

Alpha the stabiliser

The last point we discuss is the positive association of alpha oscillations with stability in visual processing. This view has been suggested by studies of multistable perception finding that people are more likely to report changes in their perception of ambiguous visual stimuli (e.g. Necker cubes) during periods of reduced alpha power (e.g. Isoglu-Alkac *et al.*, 2000; Mathes *et al.*, 2010). Such reductions in alpha have been suggested to reflect destabilisation of ongoing perceptual interpretations, facilitating shifts towards alternative interpretations (Strüber & Herrmann, 2002; Piantoni *et al.*, 2017). Decreases in alpha power are similarly reported when people switch their attention between different visual tasks (Poljac & Yeung, 2012; Foxe *et al.*, 2014), while increases in alpha power are observed when people maintain information in visual working memory (Jensen *et al.*, 2002; Jokisch & Jensen, 2007). Although this latter finding could reflect suppression of irrelevant visual processing, it may also suggest a positive role for alpha in maintaining ongoing processing (Johnson *et al.*, 2011). In addition, slow event-related potentials, evoked during the retention of information in visual working memory (known as ‘contralateral delayed activity’), have been associated with asymmetric amplitude modulations of the peaks and troughs of alpha oscillations (Mazaheri & Jensen, 2008; van Dijk *et al.*, 2010). This finding again suggests an involvement of brain activity at alpha frequencies with sustained maintenance of ongoing, visual processing.

One reason why alpha oscillations may promote stability in visual processing is that these rhythms are fundamentally bistable in nature. In resting state EEG recordings, alpha rhythms have been found to shift periodically between high- and low-amplitude modes (Freyer *et al.*, 2009). This is consistent with computational models in which alpha switches between distinct attractor states, with one representing a default state of reduced stimulus processing, and the other facilitating increased stimulus processing (Lundqvist *et al.*, 2013). Such bistability in alpha oscillations may aid stability in visual attention as switches between two discrete, neural states should require greater changes in neural excitation than gradual changes across a continuum of neural states. In addition, it is also interesting to note that beta oscillations, while also associated with a large number of cognitive processes (e.g. Etchell *et al.*, 2014; Hanslmayr *et al.*, 2014; Bastos *et al.*, 2015), have been linked with the

maintenance of sensorimotor processing (Engel & Fries, 2010) and are thought to be an intrinsic property of motor cortex (Rosanova *et al.*, 2009; Ferrarelli *et al.*, 2012). As alpha oscillations may be an intrinsic property of visual cortex (Rosanova *et al.*, 2009; Hindriks *et al.*, 2015), this could also suggest a general association between stability of processing in a given brain region and neural activity at the resonant frequency of that region.

Conclusions and future directions

We have reviewed evidence associating alpha oscillations with five distinct aspects of neurocognitive functioning. To summarise, alpha oscillations are negatively associated with visual attention, with increases in alpha power strongly associated with reductions in visual processing. This may reflect the involvement of alpha oscillations in suppressing visual activity. Nevertheless, this suppression is fundamentally periodic and may also play important roles in regulating visual perception. This point is supported by evidence linking alpha oscillations to the segregation of visual inputs into discrete events, as well as by the finding that delivery of flickering lights at alpha frequencies during eyes-closed rest can elicit strong visual experiences. One way in which alpha may support perception is by facilitating the communication of top-down predictions to visual cortex. Intriguingly, alpha oscillations may periodically regulate the influence of top-down predictions and bottom-up inputs on visual processing. However, alpha oscillations also associate with communication across the brain more generally, particularly through long-range phase synchronisation, but also via travelling waves that propagate between frontal and posterior brain regions. Lastly, alpha oscillations may play important roles in stabilising visual processing.

A key question highlighted by this summary is why alpha should exhibit such diverse associations with such a wide range of cognitive functions. One possibility is that distinct characters of alpha oscillations are associated with subtly different peak frequencies. For example, working memory has been positively associated with power in the upper alpha band (i.e. 10–13 Hz), but not the lower band (i.e. 7–10 Hz; Klimesch, 1999; Nenert *et al.*, 2012). However, in conflict with this view, many studies have found variable associations between alpha oscillations and cognition using near-identical frequency bands (e.g. Kelly *et al.*, 2006; Stenner *et al.*, 2014; Piantoni *et al.*, 2017). Another possibility to explain the diverse links between alpha and cognition relates to the variety of ways in which alpha oscillations can vary independently (e.g. power, phase, long-range synchronisation). Specifically, different electrophysiological features of alpha may correlate with distinct cognitive functions. Of relevance to this point is the finding that, whereas alpha power in visual cortex typically associates negatively with visual attention (i.e. alpha the inhibitor), alpha phase synchronisation between visual and frontal cortex associates positively with visual attention (i.e. alpha the communicator; Doesburg *et al.*, 2009). Nevertheless, it is less apparent how other cognitive functions of alpha (e.g. stabilisation) might associate with such specific, electrophysiological features of alpha. Furthermore, many features of alpha have been found to covary with a variety of cognitive functions. For example, increases in alpha power alone have been associated with attentional inhibition, perceptual stability, and top-down predictions (e.g. Kelly *et al.*, 2006; Stenner *et al.*, 2014; Piantoni *et al.*, 2017). Further research in this area is clearly needed. Finally, it is also possible that, although alpha oscillations may be discussed as a singular phenomenon, they in fact reflect a number of distinct, neural processes (e.g. Walter, 1953). This idea is consistent with evidence that alpha oscillations can be generated by a variety of cellular mechanisms (Wang, 2010; Womelsdorf *et al.*, 2014). The idea is

also supported by findings that the association between alpha power and activation in different regions of the brain changes depending on whether alpha is recorded during eyes-closed or eyes-open rest (Zou *et al.*, 2009; Mo *et al.*, 2013). In addition, although alpha power in occipital cortex correlates negatively with visual attention, alpha power in inferotemporal cortex has been found to correlate positively with visual attention (Mo *et al.*, 2011). Consequently, it may be that a number of independent alpha oscillations are generated in different regions of the brain and in different cognitive contexts. These considerations indicate that it may be misguided to study broad links between cognitive functioning and ‘alpha oscillations’, considered as a singular phenomenon.

A central question posed by this last point is how different subtypes of alpha could be distinguished in experimental settings. One approach could be to measure alpha oscillations during simultaneous collection of functional neuroimaging data (e.g. Laufs *et al.*, 2003). For example, we would predict that the peak frequencies of alpha oscillations in posterior cortex would associate more strongly with the temporal resolution of visual perception when those oscillations are recorded during periods of increased activity in visual thalamus. This is due to the suggested role the lateral geniculate nucleus in segmenting visual inputs into distinct subgroups (Lőrincz *et al.*, 2009). We would therefore expect to observe a moderating effect of thalamic activation on, for example, the positive association between an individual’s peak alpha frequency and their ability to classify two quick flashes as separate events (Samaha & Postle, 2015). Such a finding would suggest that a subtype of alpha, which associates primarily with ~10 Hz oscillations in visual processing, could be distinguished by its positive association with thalamic activation. In contrast, we would also predict that changes in alpha power observed during periods of increased fronto-posterior network connectivity (e.g. assessed using magnetoencephalography or functional magnetic resonance imaging) would be more associated with communication of top-down predictions to visual cortex. For example, it may be that previously described associations between alpha phase and communication of sensory predictions (Sherman *et al.*, 2016) would be clearest when functional connectivity between frontal and occipitoparietal regions is high. This would again suggest that a subtype of alpha, associating primarily with top-down processes in the brain, could be distinguished from other subtypes by its positive association with fronto-posterior connectivity.

Lastly, it is important to consider whether alpha oscillations play mechanistic roles in cognitive processing, or if they are simply epiphenomena of large-scale brain activity. Although we associate alpha oscillations with a range of cognitive functions in this article, we base these associations primarily on correlational rather than causal evidence. It is therefore difficult to determine whether alpha oscillations are central to the engagement of these cognitive functions, or if they are just common by-products of unrelated neural processes. Several methods could be used to address this issue in future research, including rhythmic transcranial magnetic stimulation and transcranial alternating current stimulation. These techniques can experimentally manipulate the power and phase of alpha activity (Thut *et al.*, 2011; Helfrich *et al.*, 2014) and have supported associations between alpha rhythms and both visual inhibition (Romei *et al.*, 2010) and the temporal resolution of perception (Cecere *et al.*, 2015; Minami & Amano, 2017). However, such techniques are limited by significant variability in their effects across diverse groups of people (e.g. Krause & Cohen Kadosh, 2014; Wiethoff *et al.*, 2014). Alternatively, the contribution of alpha oscillations to cognition could be investigated by evoking these rhythms using flickering images. Such flickers, when delivered at ~10 Hz, can entrain the phase of ongoing alpha oscillations,

allowing researchers to study causal associations between alpha phase and visual processing (e.g. Notbohm *et al.*, 2016). For example, associations between alpha and rhythmic fluctuations in visual attention have been supported by studies finding that, when people are briefly shown ~10 Hz visual flickers, their ability to detect subsequently presented visual stimuli oscillates in phase with that flicker (Mathewson *et al.*, 2012; Spaak *et al.*, 2014).

An intriguing line of future research could extend this approach to assess the roles of alpha in top-down predictions, given the previously described results of Sherman *et al.* (2016). These researchers found that an intermediate alpha phase position (0°) was associated with a more liberal response bias to threshold visual targets when these stimuli were expected, but a more conservative bias when these targets were not expected (Fig. 1H). To further investigate this effect, a study could be run in which ~10 Hz flickers are again presented before the delivery of threshold visual stimuli (e.g. as in Spaak *et al.*, 2014). However, some superficial aspect of these flickers (e.g. colour) could signal the likelihood that a threshold stimulus would subsequently be presented. If prior expectations do indeed influence the association between alpha phase and threshold visual detection, we would expect to observe anti-correlated alpha oscillations in stimulus detection performance following the presentation of visual flickers that indicate an upcoming stimulus is either likely or unlikely. Given the association between top-down processes and acetylcholine, one might also predict that this behavioural effect would be enhanced by administration of a cholinergic agonist (as in Bauer *et al.*, 2012). Such a result would provide evidence that alpha oscillations are mechanistically involved in rhythmic communication of predictions to visual cortex. However, it is difficult to imagine how such a methodology could be applied to determine the involvement of alpha oscillations in other cognitive functions that are less easily measured following presentation of short visual flickers (e.g. long-term stability of perceptual states). Thus, despite substantial progress, there clearly remains much to be learned about alpha oscillations and their roles in neurocognitive functioning. We hope this review can galvanise other researchers to further investigate these dominant and multifaceted rhythms of the human brain.

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Conflict of interest

The authors declare no competing financial interests.

Author contributions

The manuscript was conceived and written by MSC. RCK and NY gave comments on the structure and wording of the manuscript.

Data accessibility

No primary data are reported in this review.

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