Slower resting alpha frequency is associated with superior localisation of moving targets

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Abstract

We examined the neurophysiological underpinnings of individual differences in the ability to maintain up-to-date representations of the positions of moving objects. In two experiments similar to the multiple object tracking (MOT) task, we asked observers to monitor continuously one or several targets as they moved unpredictably for a semi-random period. After all objects disappeared, observers were immediately prompted to report the perceived final position of one queried target. Precision of these position reports declined with attentional load, and reports tended to best resemble positions occupied by the queried target between 0 and 30 ms in the past. Measurement of event-related potentials showed a contralateral delay activity over occipital scalp, maximal in the right hemisphere. The peak power-spectral frequency of observers' eyes-closed resting occipital alpha oscillations reliably predicted performance, such that lower-frequency alpha was associated with superior spatial localisation. Slower resting alpha might be associated with a cognitive style that depends less on memory-related processing and instead emphasises attention to changing stimuli.

1. **Introduction**

Perceiving dynamic scenes involves maintaining up-to-date visual representations of the world. We investigated how it is that some individuals perform better at this task than others. Specifically, we examined the neurophysiological basis of keeping up-to-date representations of the changing positions of moving objects. In the multiple object tracking (MOT) task, in which observers attempt to keep track of the identities of moving target objects amongst distractors, it is becoming clear that individual differences affect performance: factors include age (Sekuler, McLaughlin & Yotsumoto, 2008; Trick, Jaspers-Fayer and Sethi, 2005; Trick, Perl and Sethi, 2005) cognitive development (Ho et al., 2006; O'Hearn, Landau and Hoffman, 2005), training and expertise (Allen et al., 2004) and computer gaming (Green and Bavelier, 2006). How exactly these factors modify tracking ability is not yet clear, although stable individual differences in tracking skills do emerge: Alnæs et al. (2014) showed that individual differences in cognitive effort during MOT (measured by pupillometry) predict brain activity in dorsal processing areas, which are known to be active during MOT (Culham et al., 1998). Huang, Mo and Li (2012) showed that tracking performance relates to a general cognitive measure, although it appears that specific mechanisms of individual differences in tracking performance are yet to be identified. Most MOT studies use a coarse measure of spatiotemporal object representation: knowledge about whether a particular object is or is not a target. Instead, we here use a position monitoring task (Howard and Holcombe, 2008; Howard, Masom and Holcombe, 2011) which provides a more direct and fine-grained measure of moment-to-moment spatial representations by asking observers to report objects' final perceived positions.

To investigate the neural basis of MOT performance, some studies have introduced brief probe flashes on targets and distractors during tracking, recording the event related potential (ERP) response to these flashes. Attentional modulation of ERP amplitude has been demonstrated in these studies. For example, Drew et al. (2009) showed P1 and N1 enhancement to flashes on targets compared to those on distractors. Furthermore, individuals with greater tracking capacity showed greater differentiation of amplitude between targets and distractors. Doran and Hoffman (2010) also found N1 amplitude greater for flashes on targets than those on distractors, and others have shown that this attentional modulation depends on tracking load (Sternshein, Agam & Sekuler, 2011). Using a method similar to that of Belmonte (1998), Störmer et al (2013) displayed flickering stimuli to elicit steady-state visual evoked potentials (SSVEPs) tagged with different frequencies for targets and distractors. They found greater amplitude in response to this flicker on targets than on distractors and greater amplitude when tracking more targets. However, neural response to such luminance changes superimposed on objects is not a direct measure of the neural response to the objects themselves.

A more direct measure utilised by Drew and colleagues is the contralateral delay activity (CDA), a sustained, lateralised negativity elicited at posterior scalp sites during tracking. Drew and Vogel (2008) showed that CDA amplitude increases with target number, and that individuals showing high capacity for the task manifest a greater (more negative) CDA response. CDA amplitude also appears to respond to load demands during tracking (Drew et al., 2012) and hence can provide an online measure of tracking activity without recourse to introducing flashes or other probes.

Outside of MOT, some have controversially proposed that perception itself appears to be a rhythmic process oscillating at 10 Hz (VanRullen and Macdonald, 2012). This conjecture is supported by evidence that detection of stimuli is well predicted by the phase of neural

oscillatory activity in the theta and alpha bands (Busch, Dubois and VanRullen, 2009). Further, the phase of ongoing alpha oscillations predicts perception of brief or hard-to-detect stimuli (Matthewson et al., 2009). In the position monitoring task, moving objects disappear and observers are immediately queried as to the final perceived position of one of the objects. Therefore, if alpha phase determines the times at which representations are periodically updated, then performance should be related to the phase of ongoing alpha activity at the moment of stimulus offset.

High-amplitude alpha oscillations are induced with eyes closed; this resting alpha activity is considered to reflect an internally directed state (see Hanslmayr et al., 2011). Robust individual differences in peak alpha frequency (PAF) ranging from around 8Hz to 12Hz have been linked to a number of cognitive variables including memory (Clark et al., 2004; Klimesch, 1997; Klimesch et al., 1990), reading ability (Suldo, Olson and Evans, 2001) and verbal abilities (Anokhin and Vogel, 1996). Therefore it might be the case that individuals with higher-frequency resting alpha update visual representations more frequently, allowing more accurate performance on the position monitoring task. Since this hypothesis has not to our knowledge been tested before, we measured individuals' PAF at rest, and their continuous EEG whilst performing a position monitoring task. In Experiment 1, observers monitored either one or both of two target objects and in Experiment 2, observers monitored between 1 and 4 of 4 moving objects displayed on each trial. Observers reported the final perceived position of one of the targets, and mean spatial error was recorded.

2. Method Experiment 1

The position monitoring task was used, in which observers attended to either one or both of two moving discs. After a short movement phase, both discs disappeared and observers were queried as to the final position of one of the discs (see Figure 1). On trials where observers were attending to one disc (one-target trials), this attended disc was queried. On trials where observers attended to both discs (two-target trials), they were randomly queried as to the final position of one or the other disc. In other words, on every trial, participants either attended to one disc while it moved unpredictably, and then reported its final position, or they attended to two discs while they moved unpredictably, and then reported the final position of one of the two. Stimuli were displayed on a Mitsubishi Diamond Pro 920 colour CRT monitor, driven at 85Hz, with a resolution of 1200×1600 pixels. Observers sat approximately 57cm from the screen, and responses were made using a keyboard and mouse. The experiment was created using PsychoPy (Peirce, 2007).

Prior to the task, we measured observers' peak alpha frequency (PAF) at rest. Observers were instructed to sit still and to relax with their eyes closed while EEG was recorded for two minutes. We also recorded continuous EEG during the task itself. After the task was explained, observers were given a practice block of around twelve trials and in no case more than 24 trials. Observers participated in ten blocks of 40 trials over approximately 50 minutes, within which one-target and two-target trials were randomly intermixed.

2.1 Observers

Fifty observers (38 females) took part in the study and were compensated with either course credits or a £15 online shopping voucher. Ages ranged from 18 to 35 (M=21.4, SD=3.91). All observers were right-handed and reported having normal or corrected to normal vision, and no history of neurological disorders. As a result of the long testing sessions caused in part by setting up the 128-channel EEG recording, 12 observers withdrew before the end of the experiment and their data were not included in subsequent analyses, resulting in a sample of 38 observers.

2.2 Procedure

At the start of each trial, observers were presented with a black (0.05 cd/m^2) fixation point (0.2° diameter) against a uniform grey background (20.20 cd/m^2) with two solid white (45.08 cd/m^2) areas subtending 8° x 8° presented one degree eccentric to the left and right of the fixation point. 0.2° beyond the outer edge of each of these two movement areas was the inner edge of a solid grey (14.9 cd/m^2) vertical bar (0.2° x 8°) that served as a placeholder for subsequently presented cues. Observers were instructed that cues would be either black or white for the duration of the experiment. At the start of every trial, placeholders changed to the cue colour – either white (45.08cd/m^2) or black (0.05cd/m^2) – for 400 ms plus up to 200 ms random uniformly distributed jitter (i.e., 400 ms to 600 ms total cueing time). Either one or both of the areas was cued, randomly with probability 50% two cues, 25% left single cue and 25% right single cue on each trial. One static dark grey disc (0.5° diameter, 7.00 cd/m^2) was presented at a randomly selected location within each white movement area.

Offset of the cue(s) was followed by a 300-400 ms delay (again with random, uniformly distributed jitter), after which the discs began to move pseudo-randomly within their respective areas. Discs continued to move for a period randomly jittered between 2000-4000

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ms before disappearing. Horizontal and vertical components of motion were calculated independently, with positive values representing upward or rightward motion. Initial velocity and acceleration parameters were chosen randomly from fifty uniformly distributed values between -1.3 and 1.3 °/s, and -12.75 and +12.75 °/s², respectively. If a disc's horizontal or vertical velocity exceeded 4 °/s, its acceleration in that dimension would reverse direction. On every frame brought about by a screen refresh, each disc's acceleration along the horizontal and vertical components of velocity had an independent 0.05 probability of being reselected at random from the range of acceleration values. During the motion phase, if a disc reached the edge of these areas, its velocity would reverse, appearing to 'bounce' off the boundary according to the law of perfect elastic collisions.

Immediately after the discs' offset, a cue placeholder brightened/darkened to query one disc. Observers used the mouse to move a probe disc (which appeared as a cursor identical in appearance to the disc itself) to indicate by means of a mouse click the final perceived position of the queried target. To avoid apparent motion effects, the probe disc only appeared after the discs' offset and following an initial mouse movement. It appeared on the next frame immediately after mouse motion was detected and appeared at the location determined by the current mouse position. Immediately following the response, feedback was provided by means of presenting the queried target in its veridical final position before the next inter-trial interval.
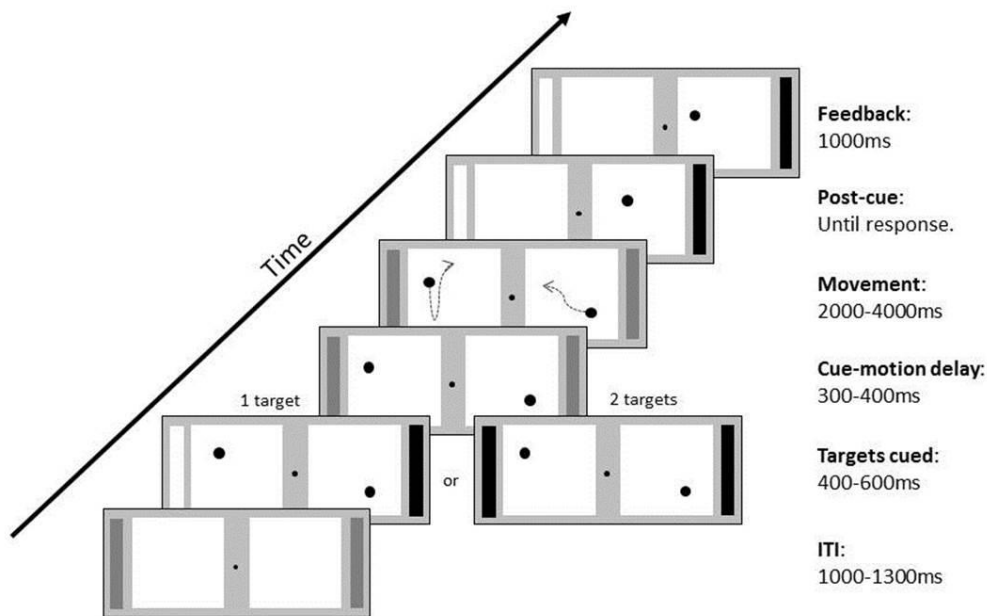

Figure 1: Example timeline of a trial in Experiment 1 (in this example observers are told that cues are black).

2.3 Behavioural Analysis

For each trial, we calculated the spatial error of the response which is the distance in degrees between the reported final position of the queried target and its veridical final position. Responses that fell outside of the target movement area were excluded (0.46% trials). One of the 38 observers' mean error was poorer than 3 standard deviations from the group mean and was therefore excluded from the performance data. Effect of attentional load was assessed via

a paired-sample *t* test contrasting spatial errors between the one-target and two-target tracking conditions.

Perceptual lags (see Howard and Holcombe, 2008; Howard, Masom and Holcombe, 2011) were calculated by comparing the reported final position of the queried target with its veridical final position, and also with the positions it had occupied on the frames leading up to its disappearance, as well as with extrapolated positions that it would have occupied had it continued moving after its diappearance. To find the perceptual lag magnitude, we found the average time (quantised in units of video frames, i.e. 11.76 ms) for each observer at which reports best matched the veridical final positions of the queried target (within the range of 250 ms before offset to 150 ms after offset). For example, if the reported final position were closest on average to the position occupied by the queried target ~50 ms before its disappearance, then this comparison would represent a perceptual lag of ~50 ms. If reports best resemble where the queried target would have been had it continued moving for an additional ~20 ms, then this comparison would represent the opposite of a perceptual lag, namely extrapolation by ~20 ms.

2.4 Task-related Electrophysiological Recording

EEG was recorded using a 128-channel ActiveTwo (Biosemi, Netherlands) amplifier. Data were acquired using 128 Ag/AgCl active pin electrodes at 2048 Hz and digitized with 24-bit resolution. Electrodes were placed in the Biosemi ABC configuration using an elastic cap fitted to the observer's head. Two flat sensors were placed ~2cm laterally to the external canthi of each eye, and one on the left cheek (to measure horizontal and vertical EOG, respectively). Two flat sensors were also placed on the left and right mastoids. Data were referenced online using a CMS/DRL feedback loop with online low-pass filtering performed in the analogue-digital-converter (5th order sync response with a -3dB point at 1/5th of the sampling rate). Digitised EEG was transferred to the data acquisition computer via an optical cable and viewed online using ActiView software (Biosemi).

Continuous EEG data were imported and processed using bespoke scripts and those from EEGLAB (Delorme and Makeig, 2004). All sensors were re-referenced offline to the algebraic mean of the left and right mastoids. Data were down-sampled offline to 512 Hz and high-pass filtered at 0.01 Hz using a linear finite impulse response filter. Any trial on which the EOG recorded more than one positive or negative change of greater than 25 μV within any given 75ms window after onset of the cue and before the end of the trial was identified as an eye movement and excluded. 23.3% of trials were excluded in this manner. AC power line fluctuations (50 Hz and its harmonics) were reduced using the Cleanline EEGLAB plugin (Mullen, 2012) which adaptively estimates and removes sinusoidal artefacts using a frequency-domain (multi-taper) regression technique with a Thompson F-statistic for identifying significant sinusoidal artefacts. Independent component analysis (Infomax ICA; Bell and Sejnowski, 1995) was applied to continuous EEG to identify neural components contributing to the observed scalp data. Ocular components such as blinks were identified by low-occurrence, non-time-locked transient fluctuations with strong positivity or negativity towards the front of the scalp, and were removed from the data. Noisy channels were identified by visual inspection and interpolated spherically.

To examine the ongoing processing during the task, data were epoched from -2000ms to 0ms relative to motion offset, and were baseline-corrected by subtracting within each channel to the average voltage of the 200ms immediately preceding the cue onset (pre-trial). Epochs

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were visually inspected and any containing clear artefacts were rejected from further analyses. Data were then low-pass filtered at 50 Hz, using a linear finite impulse response filter. The following left and right hemisphere electrodes were included in these analyses, based on previous sites used for similar analyses of position updating (Drew, Horowitz, Wolfe & Vogel, 2011; Drew, Horowitz & Vogel, 2013; Drew & Vogel, 2008): left A7, A8, A9, A15, A16, A17, D29, D30 and D31, right A28, A29, A30, B4, B5, B6, B7, B11, B12 and B13. These channels of interest were averaged together within each hemisphere.

EEG data from 7 observers were excluded because they had at least one condition with fewer than 40 trials remaining after rejecting epochs with eye movements or EEG artefacts. A further 3 observers were excluded because their data sets did not make it through all stages of preprocessing, due to failure of independent component analysis to converge to timely termination, leaving 28 observers included in the analysis of ongoing electrophysiological recording during the task.

Voltage integrated across the recording epoch was subjected to a 2x2x2 (hemisphere: left, right x queried hemifield: left, right x number of targets: 1, 2) repeated measures analysis of variance.

2.5 Peak alpha frequency (PAF)

Power spectral density was calculated (using Welch's power spectral density estimate) for channels A15, A23 and A28 (equivalent to O1, Oz and O2 and based on previous similar analysis (Cecere, Rees and Romei, 2015), and the resulting spectra averaged across channels. Peak resting occipital alpha (PAF) was calculated as the frequency with the greatest mode, and then examined for correlation with spatial error and with perceptual lag, across subjects. Power of ongoing activity at O1 and O2 sites was calculated for the final 1000 ms of the period of discs' motion by averaging the absolute power across the range +- 2Hz around the individual's PAF, excluding data from one individual whose PAF fell outside the 8-12 Hz range. As for task-related electrophysiological recording, data from 3 observers were excluded due to failure of full preprocessing to complete, resulting in a sample of 34 for the PAF analysis.

To examine any relationship between performance and the absolute phase of ongoing alpha oscillations during the trials, phase was computed in the time domain by identifying the temporal offset that maximised correlation of the single-trial EEG against a sine wave matched to frequency of the individual subject's PAF, within a sliding window ending at the time of stimulus offset. We then examined the relationship between performance on any given trial, and the phase of alpha oscillations from the occipital electrode that was contralateral to the queried target, at the moment it disappeared from the screen. For Experiment 1 and for Experiment 2, we used 9 phase bins (each 40° wide across the 360° range of possible phases).

We also investigated the possibility that the ideal phase angle might vary between individuals, and therefore conducted an analysis similar to that reported by Busch, Dubois and VanRullen (2009). For this reason we bifurcated all trials for each observer according to each of 9 bifurcation indices (e.g. to give two bifurcation range examples: 1) 0-179.9° contrasted with 180-359.9°, or 2) 40-219.9° contrasted with 220.0-39.9°) and looked for differences in mean error magnitude between the two halves of their total bifurcated sets of trials. We then identified, on an observer-by-observer basis, the most ideal of these 9

bifurcation indices, that is, the bifurcation index that maximises the difference between the two halves of the dataset. These performance differences from each individual's ideal bifurcation index were then compared against the mean of the differences from all 9 bifurcation indices for each individual. Note that if there were an ideal phase for each person that differed between individuals (e.g. for one person being 10° and for another being 50°), then this analysis would reveal a significantly greater set of differences for the ideal bifurcation index than for all indices averaged together.

However, since this analysis may allow any differences between bifurcation indices that arise by chance to be identified as apparently ideal, we conducted an additional, stricter test using simulated data sets. We ran a permutation test of 10,000 reshuffled datasets, where the phases and error magnitudes for each observer were randomly associated with one another, destroying any real association between phase and performance. We examined whether or not the ideal phase analysis produced a greater association between phase angle and performance for the real data set than these shuffled simulated datasets, in order to assess whether indeed there is any evidence for an ideal phase angle for ongoing alpha oscillations at stimulus offset.

3. Results Experiment 1

3.1 Behavioural performance

Overall, mean error magnitude was 0.83° (*SD*=0.20°) away from the queried targets' veridical final positions. There was an effect of attentional load (see Figure 2), such that mean error magnitudes were smaller, and therefore responses were more precise (t(36)=-10.61, p<.001) when monitoring only one target (*M*=0.67°,*SD*=0.20°) than when monitoring two targets (*M*=0.96°,*SD*=0.25°).

Fig 2: Mean error magnitudes for monitoring one and two targets. Error bars represent standard errors, N = 37.

To examine whether there were any overall order effects in the data we compared observers' performance during the first (M=0.838, SD=0.224) and second half (M=0.855, SD=0.217) of trials, and no such differences were observed (t(36)=0.72, p=0.48).

No observer's mean perceptual lags were more than 3 standard deviations from the group mean, for any condition. On average, observers exhibited a perceptual lag of 6 ms (*SD*=30 ms) for monitoring one target and 30 ms for monitoring two targets (*SD*= 30 ms), demonstrating an increase in perceptual lag with attentional load (t(37)=4.50, p<.001), shown in Figure 3 (lefhand panel).
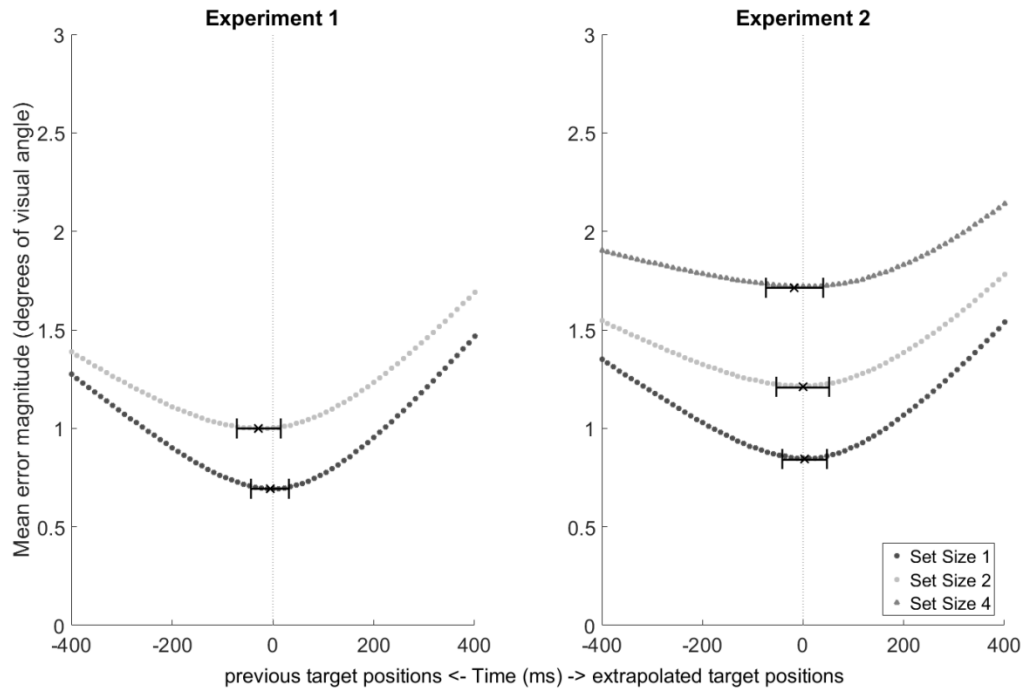
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Figure 3: Perceptual lag magnitudes across Experiment 1 (left, N = 38) and Experiment 2 (right, N = 33) (error bars indicate standard errors of between-subjects lag magnitudes). Each dot represents the mean distance between the reported position and the position occupied by the queried target at that time. Minima on these curves indicate perceptual lag values and are the times at which reports best matched the position of the queried target.

3.2 Task-related electrophysiological analysis

There was a main effect of electrode hemisphere ($F(1,27)=20.929$, $p<.001$) with activity being more negative over right than left hemisphere. There were, however, no main effects of attentional load or queried target hemifield.
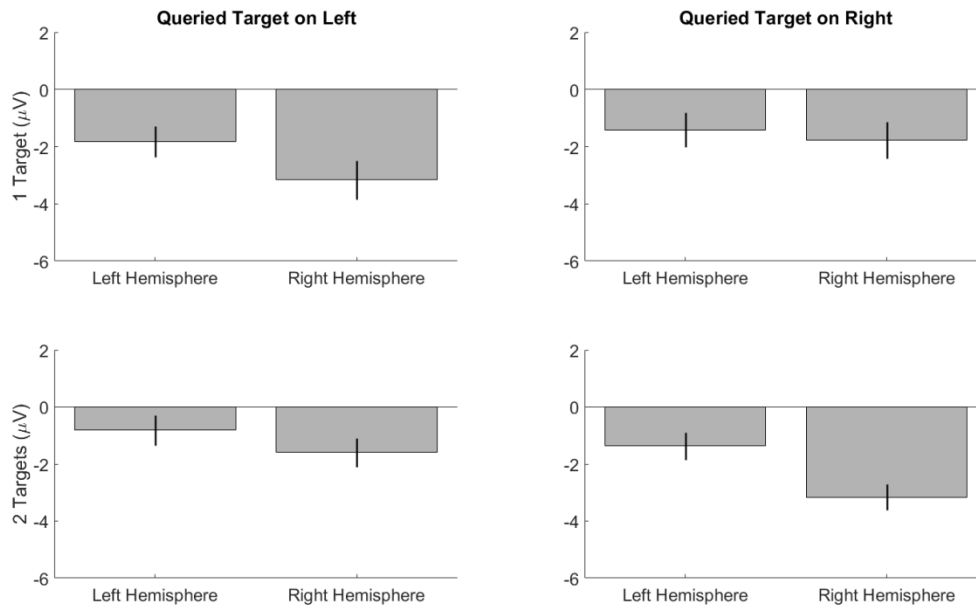
Figure 4: average negativity during the late trial epoch broken down by hemifield of the queried target, electrode hemisphere and attentional load. Error bars indicate standard errors, N=28.

Attentional load interacted with queried target hemifield (F(1,27)=11.495, p=.002): when the queried target was on the left, overall scalp potential was more negative for one-target trials (in which attention was being directed to the left hemifield solely) than two-target trials (in which attention was being distributed across targets in both hemifields; p=.037). However when the queried target was on the right, there was no such effect of attentional load (p=.193).

Complementing this single-target, left-hemifield effect on amplitudes was a three-way interaction (F(1,27)=12.164, p=.002) in which there was no difference in activity between hemispheres when one target was presented on the right (p=0.341), but right hemispheric scalp potential was more negative than left both for one target presented on the left (p=0.001) and when monitoring two targets (for both left-queried (p=0.006) and right-queried (p<0.001) targets. This was as expected because the left or right post-cue appears just after the end of the epoch and thus cannot influence amplitudes) – that is, right scalp was more negative than left whenever the left hemifield was being monitored. There was no interaction between attentional load and electrode hemisphere (F(1,27)=2.891, p=.101) and no overall interaction between queried target hemifield and electrode hemisphere (F(1,27)=0.006, p=.939).

3.3 Peak alpha frequency (PAF)

Observers' PAF ranged from 8.3 Hz to 11.6 Hz, with a mean of 9.99 Hz (SD=0.77 Hz). Error magnitudes correlated with PAF (see Figure 5) for one-target (r(33)=0.346, p=.045) but not two-target (r(33)=0.195, p=.270) trials. Combining both conditions, PAF remained correlated with errors (r(33)=0.357, p=0.038).
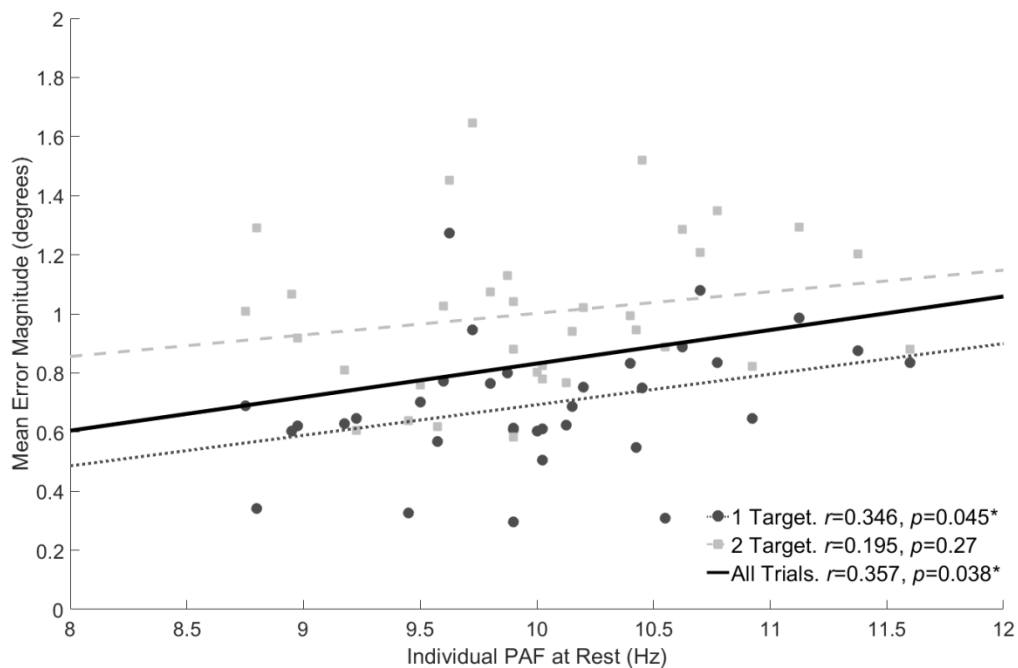
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Figure 5: Relationship between observers' occipital PAF at rest and their position monitoring performance in Experiment 1, N = 34.

PAF was not correlated with the magnitude of individuals' perceptual lags for one-target trials (r(33)=0.139, p=.412),two-target trials (r(33)=-0.002, p=.991), nor overall (r(33)=0.051, p=0.764).

For each observer, we assessed the trial-by-trial relationship between performance and occipital power in the alpha band in the hemisphere contralateral to the queried target. In two observers there was a negative relationship (p<0.01, p=0.048) and in one observer there was a positive relationship (p=0.049) but when corrected for multiple comparisons there was no overall correlation between performance and alpha power in the final second of the moving display (mean r = -0.003, mean p = 0.51).

There was no absolute phase bin for ongoing alpha oscillations at the time of stimulus offset that was associated with significantly smaller errors than the mean error (for all 9 phase bins p >=0.165). The analysis examining ideal phase did show that the ideal bifurcation index produced significantly different error magnitudes between halves of the bifurcated set of trials than the average of all 9 bifurcation indices (t(27)=10.972, p<0.01). However, in each of the 10,000 simulations from shuffled datasets, the ideal phase analysis revealed one or more bifurcation indices where performance differed between the two halves of the bifurcated simulated datasets (p<.001). Therefore there was no more evidence for the presence of an ideal individual phase for observers than there was in simulated data sets with no real association between the EEG and behavioural data.

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4. Method Experiment 2

In Experiment 2, we sought to replicate the findings of Experiment 1 in terms of behavioural performance, the relationship between performance and occipital PAF at rest and in terms of right hemispheric dominance. To investigate attentional load effects, we increased the number of targets for position monitoring on any given trial to four.

Experiment 2 was identical to Experiment 1 except for the following differences. On every trial, we presented 8 moving discs, each in its own area (6x6°) and four in either hemifield (see Figure 6). Movement areas were arranged in two vertical columns of four either side of fixation, with the inner edges 4° from fixation, and 0.1° gap between vertically adjacent areas.

At the start of each trial, all 8 discs appeared and all cue placeholders changed to black or white to indicate the location of targets on that trial (observers were instructed whether cues would be black or white at the start of the testing session, as in Experiment 1). One, two or four of the discs within one hemifield were randomly selected and indicated as targets for monitoring on every trial. In other words on every trial, participants either attended to one disc while it moved unpredictably, and then reported its final position, or they attended to two discs and then reported the final position of one of the two, or they attended to four discs and then reported the final position of one of them. All targets were presented within the same hemifield on every trial, and this hemifield was selected randomly between left or right on every trial. To reduce attention capture from luminance changes with this greater number of discs on screen than in Experiment 1, following the movement period, only one of the discs disappeared (the queried target), while all other discs continued to move until the observer made their response.

4.1 Observers

48 observers (30 females) took part in the study and were compensated with either course credits or a £15 online shopping voucher. Ages ranged from 18 to 31 ($M= 21.85$, $SD=3.37$). All observers were right-handed and reported having normal or corrected to normal vision, and no history of neurological disorders. Two of these had previously participated in Experiment 1. 11 observers withdrew before the end of the experiment and therefore their data were not included in subsequent analyses, resulting in a sample of 37 observers.
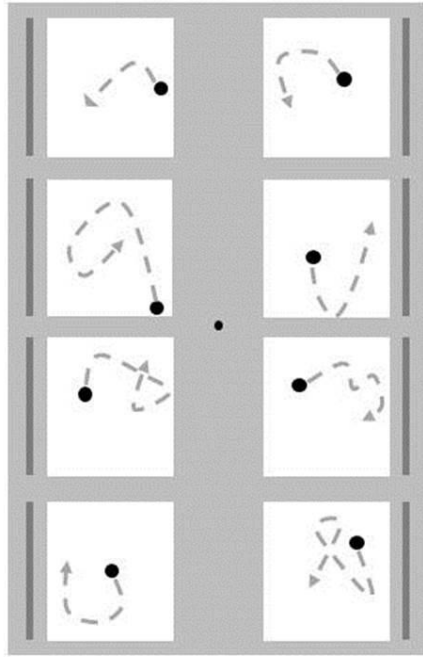
Figure 6: illustrative motion phase and screen layout for Experiment 2.

5. **Results Experiment 2**

5.1 Behavioural performance

Error magnitudes for every trial were calculated as for Experiment 1. Responses that fell outside of the target movement area were excluded (0.47% trials). Two observers whose mean error was poorer than 3 standard deviations from the group mean were excluded, resulting in a sample of 35 for performance analysis. Exclusion of trials containing eye movements as in Experiment 1 led to removal of 9.2% of trials.

On average responses were 1.28° (SD=0.29°) away from the targets' true position at offset (see Figure 7). Responses were more precise for monitoring one target (*M*=0.86°,*SD*=0.29°) than two (*M*=1.23°,*SD*=0.31°) or four (*M*=1.72°, *SD*=0.33°). This effect of attentional load (1,2 and 4 targets) on precision of position reports was confirmed with a repeated-measures analysis of variance assessing the effect of the three load levels (F(1.37,46.54)=319.04, p<.001). Post-hoc paired t-tests confirmed that mean response error was smaller for one-target than two-target trials (t(34)=14.198, p<.001) and was smaller for one than four targets (t(34)=19.48, p<.001). Errors were also smaller for two than four targets (t(34)=16.52, p<.001).
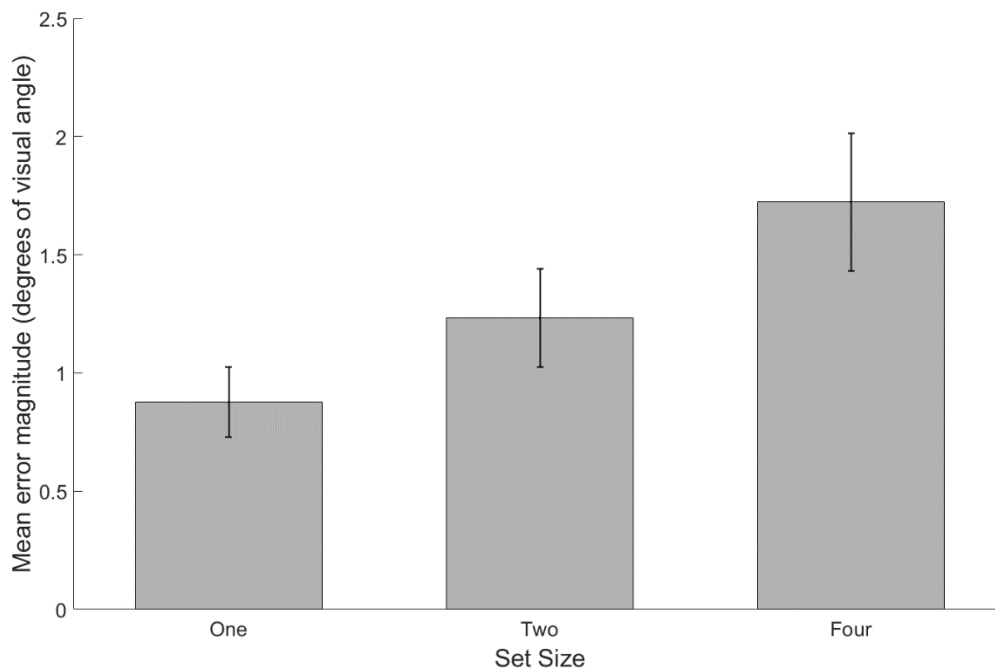
Figure 7: Mean error magnitudes for monitoring one, two or four targets. Error bars represent standard errors, N=35.

Similarly to Experiment 1, overall performance between the first (M=1.273, SD=0.296) and second half (M=1.273, SD=0.290) of trails were not significantly different (t(34)=0.024, p=.981) from one another. We also examined whether any of the 8 areas were associated with different performance levels and found that there were area effects: in a 2(left/right) x 4(vertical area locations) analysis of variance, there was no effect of side of the screen (F(1,104)=0.229, p=.635) but a significant effect of vertical area (F(3,104)=70.995, p<.001) and no interaction (F(3,104)=0.342, p=.795). Outermost (highest and lowest) areas were associated with larger errors than the innermost (middle) two areas (all ps <.001), outermost areas did not differ from each other (p=>0.99) and inner areas did not differ from each other (p>0.99). This likely indicates that targets in outermost areas suffered from poorer visibility due to their more peripheral location on the screen.

We calculated perceptual lags as described for Experiment 1. Of the total sample of 37 observers, four were excluded from lag analyses since their lag fell outside 3 standard deviations from the group mean, resulting in a sample of 33 for the lag analysis. Mean perceptual lags (shown in Figure 3 (righthand panel) were -3 ms (equivalent to 3 ms extrapolation, *SD*=30 ms) for monitoring one target, for monitoring two targets mean lag was 0 ms (equivalent to 0 ms extrapolation, *SD*=40 ms) and for monitoring four targets was 20 ms (*SD*=70 ms). A 1x3 repeated-measures analysis of variance did not reveal significant differences in these lags (F(1.50,48.08)=1.751, p=.191).

5.2 Task-related electrophysiological analysis

Two observers were excluded from EEG analysis because they had at least one condition with fewer than 40 trials remaining after rejecting epochs with eye movements or EEG artefacts, and a further seven observers were excluded because their datasets did not make it

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through all stages of preprocessing, resulting in a sample of 28 observers in the ongoing electrophysiological analyses.

We analysed ongoing EEG amplitudes in the same manner as for Experiment 1 but with a 3-way analysis of variance examining the effects of electrode hemisphere (left, right) target hemifield and attentional load (one, two or four targets). There was no effect of attentional load and no effect of the hemifield of presentation of targets. Voltage over right hemisphere electrodes (M=-3.081, SD=3.729) was overall more negative than that at left hemisphere electrodes (M=-1.713, SD=3.710), (F(1,27)=16.352, p<.001).
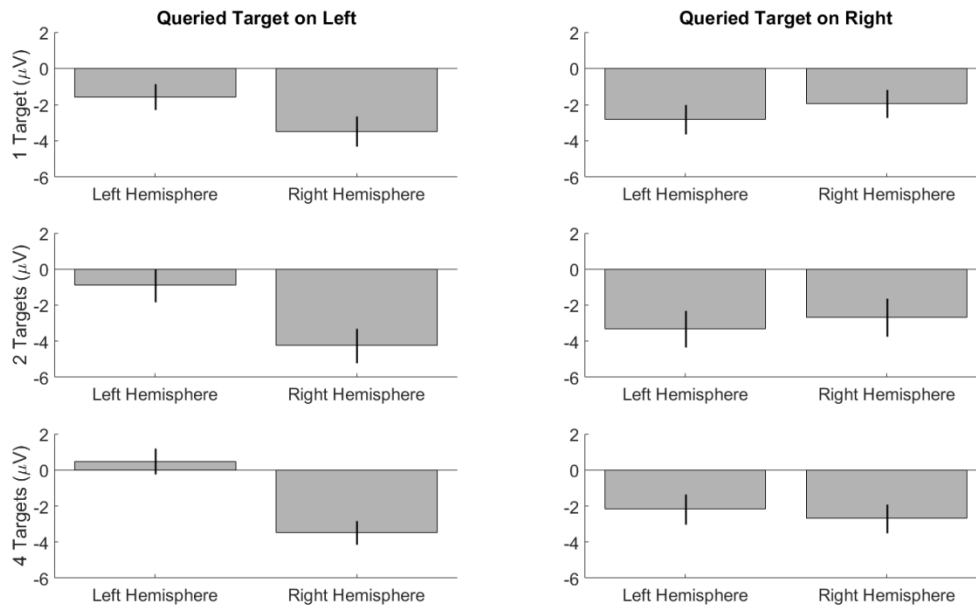

Figure 8: average negativity during the late trial epoch broken down by hemifield of targets, electrode hemisphere and attentional load. Error bars indicate standard errors, N=28.

Hemisphere interacted with attentional load (F(2,54)=28.116, p<.001): for right-hemisphere electrodes there was no effect of load whereas left-hemisphere electrodes were less negative for greater attentional loads (p=0.007). CDA was more negative over right hemisphere than left for 2 targets (p=.001) and 4 targets (p<.001), but there was no reliable difference between hemispheres for one-target trials.

There was an interaction between hemisphere and target hemifield (F(1,27)=89.199, p<.001) such that right electrodes were more negative in response to left-hemifield targets (p <0.01) although no similar relationship existed between left electrodes and right-hemifield targets. There was an additional 3-way interaction (F(2,54)=3.541, p=.036) such that the interaction between electrode hemisphere and target hemifield was more pronounced for smaller attentional loads.

5.3 Peak alpha frequency (PAF)

Peak occipital alpha frequency at rest was calculated as for Experiment 1. As for ongoing task-related EEG analyses, seven observers were excluded because their datasets did not

make it through all stages of pre-processing resulting in a sample of 30 for the PAF analysis. Observers' PAF ranged from 8.6Hz to 11.6Hz, with a mean of 9.99Hz (SD=0.78). We also examined the relationship between PAF and performance (see Figure 9). Error magnitudes were correlated significantly with PAF for one (r(29)=0.37, p=.045), two (r(29)=0.40, p=.027) and four-target conditions (r(29)=0.42, p=.019).
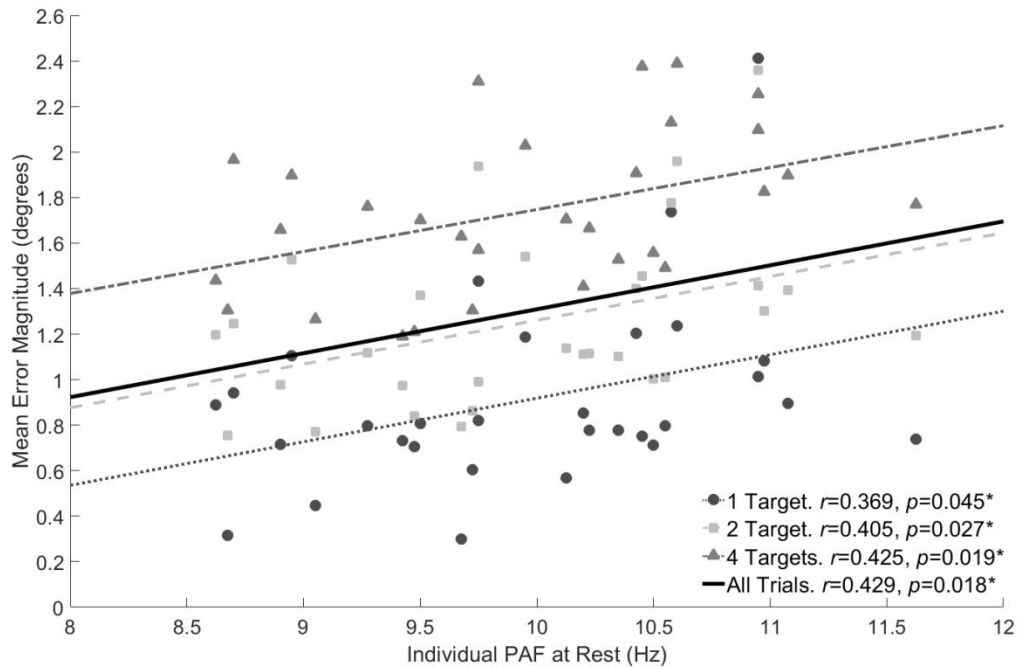

Figure 9: Relationship between observers' occipital PAF at rest and their position monitoring performance in Experiment 2, N = 30.

PAF was correlated with perceptual lag in the two-target condition (r(29)=0.489, p=.008) but not in the one-target (r(29)=-0.116, p=.556) or four-target conditions (r(29)=0.250, p=199) nor overall (r(29)=-0.054, p=0.784) This correlation between PAF and perceptual lag in the two-target condition is of potential interest because it is the two-target condition, uniquely, that presents the possibility of attending to multiple disjoint (non-adjacent) spatial locations and suppressing spatially intervening, unattended stimuli. For the 8 subjects for whom data on spatial adjacency of target locations were preserved, we undertook exploratory analyses of the effects of spatial adjacency on spatial accuracy of position reports and on contralateral EEG amplitude. Neither of these analyses revealed significant effects; however, given the low statistical power, Type II error cannot be excluded.

Since Experiment 1 was very similar to the one- and two-target conditions of Experiment 2, we compared data across the two experiments, combining data for the one-target and two-target conditions. PAF was correlated with error (see Figure 10) for one target (r(63)=0.28, p =0.024), and marginally for two targets (r(63)=0.24, p = 0.06) as well as for both of these conditions combined (r(63)=0.28, p =0.026).
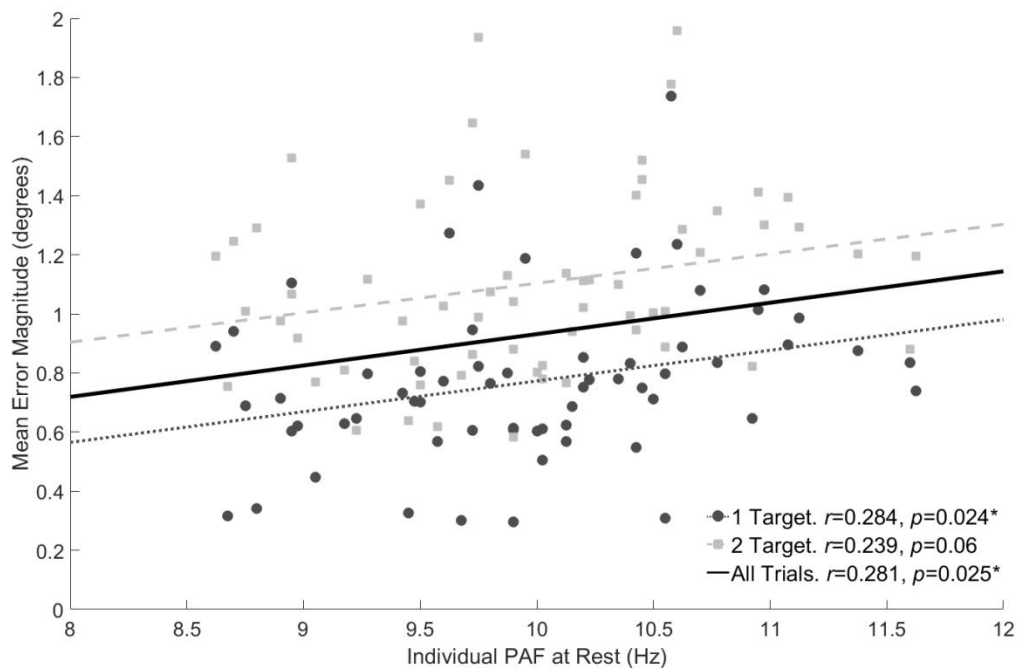
Figure 10: Relationship between observers' occipital PAF at rest and their position monitoring performance across Experiments 1 and 2, N=64.

As for Experiment 1, we assessed the trial-by-trial relationship between performance and occipital power in the alpha band in the hemisphere contralateral to the queried target. In four observers there was a negative relationship ($0.01 < p < 0.04$) and in two observers there was a positive relationship ($p = 0.002$, $p = 0.03$) but when corrected for multiple comparisons there was no overall correlation between performance and alpha power in the final second of the moving display (mean r = -0.023, mean p = 0.34).

In the same analyses as for Experiment 1, no absolute phase of ongoing alpha oscillations at stimulus offset was associated with better than average performance (for all 9 phase bins, $p \geq 0.295$). The analysis examining ideal phase did show that the ideal bifurcation index produced significantly different error magnitudes between halves of the bifurcated set of trials than the average of all 9 bifurcation indices ($t(27)=13.65$, $p<0.01$). As was the case for Experiment 1, in each of the 10,000 simulations from shuffled datasets, the ideal phase analysis revealed one or more bifurcation indices where performance differed between the two halves of the bifurcated simulated datasets ($p<.001$). Therefore here, as for Experiment 1, there was no more evidence for the presence of an ideal individual phase for observers than there was in simulated data sets with no real association between the EEG and behavioural data.

6. **Discussion**

In two experiments, we replicate previous findings (e.g. Howard and Holcombe, 2008; Howard, Masom and Holcombe, 2011) that precision of position reports declines with set size. In Experiment 1 (and to a lesser extent in Experiment 2) we show that reports exhibit perceptual lag, along with an increase in the magnitude of this lag with increases in

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attential load. In both experiments, we show the expected lateralisation of neural activity during this visual spatial task, with more negativity at right occipital sites than left, and in Experiment 2 we also see a reduced effect of load in right hemisphere. We show for the first time that individuals with peak activity in the lower frequency range of occipital alpha oscillations at rest perform better on this visual spatial task.

Greater dependence on right-hemisphere functioning for such spatial attention tasks is consistent with previous work showing right hemispheric dominance in the control of spatial attention, such as the role of right parietal cortex in hemispatial neglect (e.g. Driver and Mattingley, 1998) and activation during tracking shown for various right hemispheric sites (superior parietal lobule, lateral occipital cortex and intra-parietal sulcus, Jahn et al., 2012). It is also consistent with previous work showing attenuation of alpha activity particularly over right occipito-parietal cortex for spatial tasks (Gevins et al., 1997) and with right dominance in spatial selection and target detection (Shulman et al., 2010). Perceptual lag magnitudes varied between 0 and 30 ms, meaning that on average, reports best matched positions occupied by the queried target between 0 and 30 ms prior to its disappearance. These lags resemble those previously reported (Howard and Holcombe, 2008; Howard, Masom and Holcombe, 2011) but contrast with some evidence used to argue for extrapolated position representations (Atsma, Koning and van Lier, 2012; Iordanescu, Grabowecky & Suzuki, 2009). The reasons for these discrepant results between studies are not clear. However, some have suggested that there is some mechanism for making use of motion information for such extrapolatory processes which has a very low capacity (<=2 objects, Howe & Holcombe, 2012) and perhaps this very low capacity was not sufficient to result in detectable extrapolation for low loads in the experiments reported here.

Our finding that slower peak frequency of posterior alpha oscillations were predictive of higher performance adds to the more general debate around individual differences in attentional tasks, Individual differences in MOT tasks have previously been reported for regular action video game players (Green and Bavelier, 2006; Sekuler, McLaughlin & Yotsumoto, 2008) and for radar operators - individuals with expertise in a specific real-world position monitoring task. There are a number of potential explanations for these findings, including development and training of sustained attention and vigilance. Another possibility raised by the results presented here, is a relationship with alpha resonance. Studies examining individual differences in alpha have previously associated higher-frequency resting alpha-band activity with superior cognitive skills, such as higher general intelligence (Anokhin and Vogel, 1996). Further, PAF appears to decrease reliably with age (e.g. Osaka et al., 1999) and tracking performance for multiple object tracking tasks declines with age (Trick, Perl & Sethi, 2005). On the basis of these findings, one might expect the reverse of the results that we present here i.e. that faster resting PAF should be associated with greater precision and therefore our findings contrast strikingly with these previous PAF findings. Below we consider an explanation for the relationship between low-frequency resting alpha oscillations and superior localisation based on differences in functions associated with upper and lower frequency activity within the alpha power band.

Peak alpha frequency is a measure of relative power at different frequencies within the alpha band. An individual with greater power in the lower alpha band (<10 Hz) than the upper band (>10 Hz) will have a relatively low PAF. Low- and high-frequency alpha bands have been suggested to underlie different functions, with lower-frequency alpha activity associated with attention (Klimesch, 1997) and higher-frequency alpha associated with working memory (Angelakis et al., 2004; Clark et al., 2004; Klimesch, Schimke and Pfurtscheller, 1993; Osaka

et al., 1999), semantic processing (Doppelmayr et al., 2005; Klimesch, 1997;1999, Klimesch et al., 1997) and higher-order cognitive operations such as mental rotation (Hanslmayr et al., 2005). Across all these tasks, high alpha power at rest and in pre-task baseline periods, followed by desynchronization resulting in lower power during the task have been associated with better task performance. Peak frequency of the alpha resonance might therefore index a tradeoff between complementary cognitive styles: an attention-dominated style associated with low PAF and a working-memory-dominated style associated with high PAF. The fact that those individuals with lower-frequency PAF performed more accurately on this task than those with higher PAF suggests greater relative power in those superior individuals in the lower than the upper frequency band. Therefore, these individuals may be utilising more attentional processing than memory-related processing. As this task requires processing perceptual information to a high degree of spatial precision, and constant updating of this perceptual representation, it makes sense that individuals with greater use of attentional resources should perform better. Similarly, although observers must encode their percepts to a level that makes them available for report, there is no delay between stimulus offset and the probe prompting position reports. For this reason, attempting to store, maintain and retrieve memory representations is not likely to be a beneficial strategy. Therefore lower PAF (resulting from more power in lower than upper alpha) may be more beneficial in cases where observers attempt to accurately perceive up-to-date representations of dynamic scenes as would be the case in monitoring our environments. This difference likely arises from a prioritisation of attentional over higher-order, more semantic or more mnemonic processing. Low PAF at rest may indicate less reliance on memory-related processing, allowing observers to prioritise ongoing perceptual processing of the continuously moving stimuli presented to them.

It has been suggested that neural oscillations are associated with periodic updating of visual representations (VanRullen and Koch, 2003; VanRullen and Macdonald, 2012) and therefore that perception itself may not be temporally continuous. This view has emerged as studies have shown that the phase of neural oscillations is associated with moment-to-moment fluctuations in sensitivity to visual stimulation. For example, Busch, Dubois and VanRullen (2009) showed that successful detection of hard-to-perceive stimuli related to the phase of neural oscillatory activity in the theta and alpha bands. Similarly, Matthewson et al. (2009) demonstrated that posterior alpha phase predicts awareness for a metacontrast masking paradigm. Consistent with this, Samaha and Postle (2015) showed that resting and ongoing occipital alpha frequency predicts perception for one- versus two-flash discrimination. If individuals' occipital PAF at rest determines the frequency with which their representations are updated, then we would expect to see a relationship between phase at offset and performance. However, this is not what we see here. One possibility is that these phase-dependencies may be most related to perception of very transient stimuli, whereas ours were evolving continuously over time. Although our stimuli were changing from moment-to-moment, successive positions of stimuli are not completely independent and therefore there may be more perceptual advantage in performing some degree of temporal integration; such integration could have obscured any relationship between phase and performance.

Alpha desynchronisation in response to ongoing task demands is by definition associated with lower power (e.g. Klimesch et al., 1997; Klimesch, 1999) and is sensitive to task difficulty (Gevins et al., 1997). For example, Bompas et al. (2015) showed that occipital alpha power (amongst other dorsal oscillations) accounted for a small but reliable proportion of saccadic reaction time, with lower power linked to faster reactions. Furthermore, lower power in the alpha band has been associated with superior perceptual performance (e.g.

Ergenoglu et al., 2004; Van Dijk et al., 2008). Therefore one might expect that in our task here, lower occipital alpha power might be associated with more accurate responses. However, we find no overall relationship between occipital alpha power and performance. It may be the case that such a relationship did exist here but was not detected or it may be that the continuous updating of representations required here were the cause of these different findings.

In summary, across two experiments we find a consistent relationship between observers' PAF and their performance on this continuous position monitoring task. Individuals with slower occipital alpha activity at rest were able to report the positions of targets with greater spatial precision. In other words, the present findings may indicate a more general relationship between lower frequency posterior alpha oscillations and performance in visual monitoring tasks. Furthermore, we argue that peak occipital alpha frequency is a candidate explanatory mechanisms in understanding the emerging set of factors such as age, experience (e.g. computer gaming) and expertise that appear to be related to individual differences in such tasks of continuous perception and vigilance to changes in the environment.

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