fMRI investigations into the effect of spatial attention shifting and visual perception of separation on BOLD responses in the superior parietal lobule

PhD

School of Psychology and Clinical Language Sciences

Charlotte Mary Goodwin

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Declaration of original authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Charlotte Goodwin

Abstract

Multiple conflicting claims have been made about the function of the superior parietal lobule (SPL), but no consensus reached. This thesis investigates the functionality of the SPL by challenging existing attention shifting hypotheses and proposing an alternative visual separation hypothesis, in which the perception of changing distances between objects relative to each other is potentially supported in the SPL. Replicating Vandenberghe et al. (2001), activation was observed in the SPL for conditions containing a fixed and displacing element, and minimal activation in the conditions containing only fixed elements. However, a key condition consisting of attention shifts to a single displacing stimulus failed to activate the SPL, which was not compatible with the shifting spatial attention hypothesis. In contrast, the proposed visual separation hypothesis correctly predicted no significant activation in SPL because there was no perception of changing distances between elements. Although, for two conditions, the results could not be explained by this hypothesis: in these two conditions multiple objects displaced in unison and there were no changes in separation. It was proposed that the stimuli's abrupt displacement to new locations might be responsible for these unexpected results by disrupting the natural occurrence of adaptation. This was further explored in experiment 2, where displacing stimuli comprising of multiple elements again activated the SPL whereas smoothly translating stimuli consisting of multiple elements did not, these results supported the visual separation hypothesis. Experiment 3 explored visual separation further by examining two components: interobject distance and visual angle. Using complex visual stimuli, results showed that the SPL is particularly sensitive to relative changes to interobject distance and visual angle. Finally, these experimental results and previous ones were overlaid on a SPL parcellation (Wang et al., 2015) showing that activation produced by perceiving visual separation was not concentrated in one subregion of SPL, but rather across multiple subregions.

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And finally, to my late Grandma – I get my determination from you.

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Table 3.7.3. Individual z thresholds for each participant's data where a ROI mask was created. The masks used the *road – flow* contrast and the *EML* vs *baseline* contrast to identify the voxels that were activated in *road – flow* but were not activated in the *EML* vs *baseline* contrast. Volumes (voxels), mean of % signal change and standard deviations are also displayed for each ROI as well as the peak cluster coordinates within the ROI in mm (standard space) for condition 2 vs sustain (*triplet_teleporting*) in both the left and right hemispheres.

Chapter 1 – Introduction

1.1 What is the function of the SPL?

There have been numerous human brain imaging studies that have reported selective activation within the superior parietal lobule (SPL), and many have provided an explanation for that activation. However, while the explanations are sometimes contradictory, the different studies do not refer to each other in order to address this. The accounts for the activation have included mental rotation (Jordan, Heinze, Lutz, Kanowski & Jancke, 2001), shifting spatial attention (Vandenberghe, Gitelman, Parrish & Mesulam, 2001) and processing future heading information during self-motion (Billington, Field, Wilkie, & Wann, 2010; Field, Wilkie, & Wann, 2007). Whilst the studies have provided an explanation for the activation that they observed, for some this was not the main area of focus of the study in question. The contradictory interpretations of the results that was observed highlights the importance of defining the function of the SPL.

The aim of this thesis is to take a closer look at the SPL using functional magnetic resonance imaging (fMRI) and to investigate its function (see Figure 1.1.1.). SPL is defined in this thesis using the anatomical Harvard-Oxford Cortical Structural Atlas (Desikan, Segonne, Fischl, Quinn, Dickerson, Blacker et al., 2006; Frazier, Chiu, Breeze, Makris, Lange, Kennedy et al., 2005; Goldstein, Seidman, Makris, Ahern, O'Brien, Caviness et al., 2007; Makris, Goldstein, Kennedy, Hodge, Caviness, Faraone et al., 2006) at a threshold that gave a 20% probability or above that a voxel was in the SPL for all whole brain analysis and region of interest (ROI) masks. By firstly identifying several studies that have observed activation within the SPL and looking at the visual stimuli that were used in those studies, we will highlight the suggested explanations and will propose an alternative unifying theory for the activation that was observed in the multiple studies. Using fMRI, we conducted three experiments to investigate the role of the SPL with the aim of determining its function with regards to information processing.

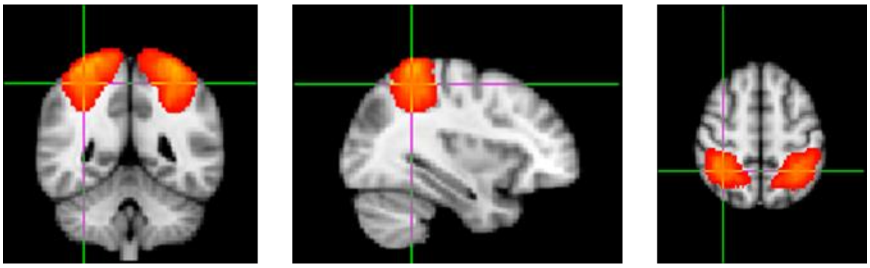

Figure 1.1.1. Unthresholded map of SPL anatomical area using Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006). Crosshairs point to MNI coordinates x34, y-48, z54

1.2 Shifting spatial attention and visual separation

One study that observed selective activation in the SPL was investigating the neural basis of shifting spatial attention. Vandenberghe et al., (2001) conducted two experiments, with the first using visual stimuli to investigate shifting of attention, and the second comparing sustained and passive attention. The visual stimuli used in the experiments consisted of a target square that would shift in a temporally unpredictable way to one of 10 pre-determined locations displayed across the vertical midline of the screen. A fixation cross was displayed centrally for the duration of the task and in the covert attention conditions the participants were asked to fixate on the static fixation cross but track and attend to the target square. Whereas in the overt attention conditions the participants were asked to fixate and attend to the target square therefore making saccades to follow the displacement of the target square to each new location. To maintain attention during the variable periods of ‘baseline time’ in which the target stimuli remained static, the participants were requested to identify a dimming event, which could occur at any time, and acknowledge it by pressing a button on a button box. Vandenberghe et al., (2001) found activation within the SPL (which they identified as the Superior Parietal gyrus) at the MNI coordinates x-24, y-57, z57 and x27, y-57, z60 for the contrast, shifting attention minus maintaining attention. This occurred regardless of whether attention was shifted covertly or overtly, and in a conjunction analysis of those two versions of the task it was impressive that the only localised brain region was in the SPL, extending into IPS. Vandenberghe et al., (2001) argued that the activation was caused by the participants shifting attention between the different locations.

However, we believe that there is an alternative explanation for the activation that was observed by Vandenberghe et al., (2001). The visual stimuli included a fixed point (the fixation cross) that remained on the screen throughout the whole experiment. The target square would then move to one of the ten different pre-determined locations across the screen’s midline. With each location change there is a change in the perceived visual separation between the fixation cross and the target square, and with each new movement the perceived visual separation would therefore change too. This would happen with each target square movement, but not during the subtractive baseline periods where the target square would stay at one location.

The fMRI contrasts that Vandenberghe et al., (2001) conducted were a comparison between shifting and sustained attention at one location. Although this could also be surmised as a contrast of perceived visual separation and where no visual separation changes are made. This suggests that the SPL could have a specialized function that supports spatial perception of separations and distances between stimuli.

What we will refer to as the visual separation theory of SPL activation is applicable when two or more objects are present, and where the visual separation, as in the distance and visual angle, between the object's changes (see Figure 1.1.2). This change can occur when there is a static object and a moving object or when there are two moving objects that are not following the same path. The behavioural relevance of such visual separation information could be in terms of action control such as reaching towards an object or programming a saccadic eye movement to shift the fovea of the eye an appropriate distance from one target to another. Determining that a change of visual separation between two stimuli or objects has occurred can also provide the brain with information that an object needs to be attended to in case a response is required.

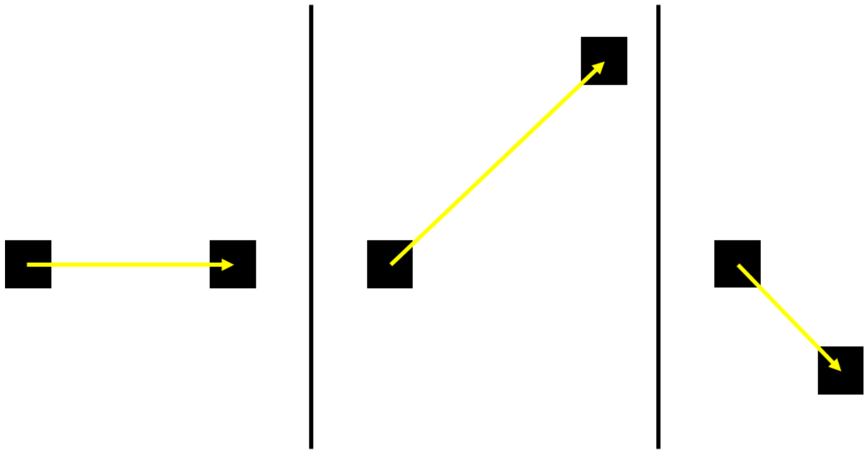

Figure 1.1.2. Changing visual separation between two objects when one or both objects move. The left square in each panel remains in the same position and the right square in each panel

is at a different location showing the varying visual separations between the two objects (depicted by the yellow line).

The visual separation theory of SPL function is a plausible alternative to Vandenberghe et al., (2001) theory of shifting spatial attention because one object (the fixation cross) remains static whilst another one (the target square) moves, which therefore changes the visual separation between them. By looking at other studies that report selective activation within the SPL, we will explore whether either the shifting spatial attention theory or the visual separation theory can provide alternative explanations of the justifications of SPL activation suggested by the authors. Many of the suggested functional specializations of the SPL that have been proposed have been based on the results of one study, generating numerous individual claims of the specific function of the SPL. It would be more likely that there is a general overarching explanation that could make sense of the individual explanations that have been provided. Either the shifting spatial attention or visual separation theories might provide a more general plausible explanation.

1.3 Other claims about the function of SPL

Here we will take a closer look at eleven different studies that reported selective activation within a similar area of the SPL (see Table 1.1.3.). The visual stimuli for each study will be described and explored in relation to the shifting spatial attention theory (proposed by Vandenberghe et al., 2001) and the visual separation theory that we have proposed. The aim is to show that either of these two theories could potentially provide a unified explanation of the SPL activation seen throughout these studies.

Table 1.1.3. Activation coordinates for the eleven studies that found activation in a similar area of the SPL. MNI* refers to talaraich coordinates that were converted into MNI coordinates using MNI<->TAL (Yale University BioImage Suite Web 1.0.0., 2018) and MNI** refers to the studies that used SPM software later than the SPM96 version where template images were in MNI space as standard and therefore the coordinates are being treated as MNI coordinates for this thesis (https://www.fil.ion.ucl.ac.uk/spm/software/spm96/).

Author	**Registered Standard Space**	**Peak Coordinates LHS**	**Peak Coordinates RHS**
Billington, J., Field, D. T., Wilkie, R. M., & Wann, J. P. (2010)	MNI	-20, -59, 62	20, -67, 59
		-28, -61, 58	
Billington, J., Wilkie, R. M., & Wann, J. P. (2013)	MNI*	-21, -68, 58	
		-24, -54, 62	
Field, D. T., Wilkie, R. M., & Wann, J. P. (2007)	MNI	-16, -66, 58	35, -48, 60
		-16, -72, 52	14, -62, 60
		-26, -54, 56	
Inman, L.A. (2014)	MNI	-18, -66, 56	26, -62, 56
Jordan, K., Heinze, H. J., Lutz, K., Kanowski, M., & Jäncke, L. (2001)	MNI	-28, -64, 48	28, -64, 48
			24, -68, 48
			24, -56, 56
			24, -64, 48
Jovicich, J., Peters, R. J., Koch, C., Braun, J., Chang, L., & Ernst, T. (2001)	MNI**	-27, -57, 69	21, -57, 72
Ohlendorf, S., Sprenger, A., Speck, O., Glauche, V., Haller, S., & Kimmig, H. (2010)	MNI		24, -54, 57
		-27, -51, 51	21, -60, 51
		-24, -57, 54	21, -57, 54
Peuskens, H., Sunaert, S., Dupont, P., Van Hecke, P., & Orban, G. A. (2001)	MNI**	-22, -60, 60	16, -70, 60
		-21, -63, 60	18, -69, 63
		-12, -60, 66	24, -60, 69
		-12, -57, 57	
Vandenberghe, R., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2001)	MNI**	-24, -57, 57	15, -63, 51
		-33, -54, 57	27, -57, 60
Wolbers, T., Hegarty, M., Büchel, C., & Loomis, J. M. (2008)	MNI	-24, -54, 52	24, -56, 56
		-30, -60, 44	32, -60, 42
Wu, Y., Wang, J., Zhang, Y., Zheng, D., Zhng, J., Rong, M., Wu, H., Wang, Y., Zhou, K., and Jiang, T. (2016)	MNI	-20, -70, 56	20, -71, 50

In a study by Field et al., (2007) who investigated future path perception and planning during locomotion, they found selective activation within a subregion of the SPL. The visual stimuli used within the study consisted of a ground plane flow in the bottom half of the screen and a solid colour at the top (to represent the sky). The two key conditions consisted of *Flow*; where the ground plane flow shows the current forward motion direction which varies over time; and the *Road* condition which has an addition of road edges that provide information about the future changes of direction of forward movement. Additional experimental conditions included *a horizontal road* control condition where the road edges were across the middle of the screen and no longer informed the observer about future travel direction. Participants were asked to provide information relating to their current perceived direction via a left or right button press. Their results showed that there was bilateral activation in the right (x14, y-62, y60) and the left (x-16, y66, z58) SPL for the *Road* condition that was not present for *Flow*. There was also no significant activation when there was a horizontal road if the road edges did not provide relevant information about the future direction of travel. The authors concluded that the future heading information that the road edges provided was responsible for the activation in this area.

Considering the Field et al., (2007) study from the point of view of the attention shifting theory in the *Road* condition the participants in this study are likely to move their gaze or covert attention to follow the road edges to try and determine their future travel direction because the road edges provide the participants with information regarding future directional changes. Whereas the ground plane flow is likely to be attended to less in the control condition. The attention shifting in the *Road* condition of the Field et al., (2007) study was subtler than that seen in the Vandenberghe et al., (2001) study and could potentially be based more on smooth pursuit than a distinct shift of attention. In the case of the *horizontal road* condition, as this was task irrelevant, it would be unlikely to be the cause of increased attention shifts above and beyond those caused by the ground plane flow. Overall, the results of this study can be seen as consistent with the attention shifting hypothesis.

Field et al., (2007) results can also be explained by the visual separation hypothesis. The *Road* condition contained a lot of relative motion, which itself consists of patterns of changing visual separation. Although the *horizontal road* condition also contained relative motion, it is likely under the visual separation hypothesis that the lack of activation that was observed in the SPL was due to the behavioural task the participants were required to do, which meant in this condition it could be ignored rather than attended to.

In a follow-up study by Billington, Field, Wilkie & Wann, (2010) activation within the subregion of the SPL was also observed. The study consisted of two experiments containing six and two experimental conditions, respectively. The authors continued to investigate the future-heading theory of SPL function by including additional conditions where the participants experience was similar to travelling in a forward motion but facing backwards. The results of the first experiment showed that SPL activation was only produced by the road edges when they were behaviourally relevant, i.e., travelling forwards. Activation was reduced when participants did not attend to the visual stimuli that were irrelevant to the task (as already discussed with the *horizontal road* condition above).

The second experiment considered whether the presence of the winding road edges visible in the distance or those visible in the foreground would activate the SPL brain region. The results were consistent with the future-heading processing theory which showed that it was the distant road edges that activated the SPL. However, the videos of the visual stimuli used in the study showed more relative motion in the distant road edges compared to those in the foreground. The extra relative motion would suggest that more attentional shifts were present in the *distant road* condition, and this would also result in an increase in changing visual separation. Therefore, both the shifting spatial attention and visual separation theories could account for the results from this study.

Billington, Wilkie, & Wann (2013) further investigated heading detection and extended this to include active steering to determine which neural areas were involved in this aspect of successful locomotion. Continuing with their visual stimuli containing a textured ground plane which moved to represent forward motion and a solid blue colour plane to represent the sky, the authors used five conditions in this study. All the conditions contained the ground plane and sky as well as numerous yellow cones that would be placed randomly on the ground plane throughout the trials – in the baseline, only the ground plane and yellow cones were present. The other four conditions consisted of two steering conditions (steer preview cones - *SteeringPv* and steer near cones -*SteeringNr*) where the participants would actively steer their course using a joystick and two heading conditions (heading preview cones - *HeadingPv* and heading near cones - *HeadingNr*) where the participants would not be actively steering but indicated the angle in which the heading direction showed, via the joystick. In the *SteerPv* and *SteerNr* conditions there were 13 additional red or blue cones added where the participant would be expected to follow instructions about which way they should pass a particular coloured cone. In the *SteerPv* condition there were approximately 6 cones visible at any one time, whereas in the *SteerNr* condition the next cone would not be introduced until the previous cone had been negotiated.

In the heading conditions, the additional red and blue cones remained although the participant was not required to actively steer around them but rather indicate the angle of movement via the joystick. The cones were visible in the *HeadingPv* condition and to make them comparable the trial movement would match one of the preceding 3 steering trials. In *HeadingNr*, the same constraints as *HeadingPv* but this time the cones would fade in as the participant progressed through the trial.

Activation within the SPL area of interest was observed in the *HeadingPv - Baseline* contrast (x-21, y-68, z58[1]) and the *SteerPv* - *HeadingPv* trials contrast (x-24, y-54, z62). The authors suggested that the activation could be related to updating of visual object location which would be used within monitoring self-motion throughout the environment when required to steer.

From the point of view of the shifting spatial attention theory, in the Billington et al., (2013) study participants in the preview (Pv) conditions were more likely to engage in shifts of attention between cone locations (because the cones were useful for performing the behavioural task) than in the baseline or near (Nr) conditions. This tendency would be accentuated in the more difficult and psychologically active steering task. The cones in the heading tasks do not require as much attention because the participants are expected to inform the angle changes in the forward motion rather than actively steer.

From the point of view of the visual separation hypothesis, the cones that were visible on the ground plane (red, blue, and yellow) provided changes in visual

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[1] To keep all coordinates within the thesis as MNI coordinates, this study that reported talaraich coordinates was converted to MNI coordinates. We used MNI<->TAL (Yale University BioImage Suite Web 1.0.0., 2018 to achieve this.

separation as the participant moved through the scene. When actively steering the participant was more likely to attend to these separations between cones in order to successfully navigate around them. On the other hand, when the participants were required to indicate passive heading changes from the pre-determined travel trajectory, the cones would be attended to less as they were not vital in the task the participant was required to undertake. Turning to the 'Nr' conditions, the number of cones seen by the participant were reduced compared to the 'Pv' conditions therefore providing less visual separation information.

Inman's, (2014) PhD thesis investigated which brain areas were involved in self-motion and expanded upon some of the visual stimuli used in Field et al., (2007) and Billington et al., (2010) that activated part of the SPL. Inman, (2014) also found activation in this area with the textured ground plane and road edges visual stimuli that featured in the previous studies, and was able to extend this to situations in which the road was replaced by two poles at different simulated distances that produced a simpler kind of motion parallax. Inman, (2014) describes this area as the dorsal medial superior parietal lobule (dmSPL) and the peak coordinates for this area were reported as (x26, y-62, z56) and (x-18, y-66, z56). The author used further experiments to determine if dmSPL was selectively involved in the processing of self-motion or had a more general function. After conducting three experiments it was determined that the dmSPL was not involved in the processing of self-motion. The author used simple two-dimensional visual stimuli (two dots) and the relative motion that occurred between the two dots were then contrasted against the motion of a single dot (control condition). The key finding was that selective activation in SPL was observed for this contrast which contained no self-motion and therefore it was possible to refute the hypothesis proposed by Field et al., (2007). With regards to the visual separation theory, the relative motion produced by the two dots created changes in visual separation between the two objects. From the shifting spatial attention perspective there would be shifting of attention between the two objects also. Therefore, the shifting spatial attention hypothesis could also explain these results.

Jovicich, Peters, Koch, Braun, Chang, & Ernst (2001) investigated which brain areas were involved in attentional load. In a tracking task the visual stimuli consisted of 10 moving balls on the screen. At the start of the trial, between two and five of these balls were indicated to the participant as the target balls, the participants then had to track the indicated subset of balls whilst fixating on a central fixation cross that was present throughout the trials. The balls moved randomly around the screen for 14 seconds before stopping and then the participant was shown one ball and had to identify via a button press whether the indicated ball was one of the original target balls that they had been shown. In a passive version of the task the balls would be present on the screen and then move randomly but none were identified for the participant to track. The baseline consisted of fixation only.

Activation was noted to have occurred bilaterally at coordinates x-27, y-57, z69 and x21, y-57, z72[2] in the SPL during the passive task versus the fixation condition (a fixation cross on a blank screen). Activation within the SPL also occurred for the contrasts tracking versus passive, and an increase in activation was noted as a function of the number of balls the participants were asked to track. The authors interpretation

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[2] Whilst Jovicich et al., (2001) reported using talaraich coordinates they used SPM99b software and since SPM96, MNI templates was used as standard (https://www.fil.ion.ucl.ac.uk/spm/software/spm96/) therefore it is likely that MNI coordinates system was used.

of these results are that the SPL (as well as other areas that coactivated with it) are important for selective visual attention that is necessary when partaking in a covert visual tracking task. (Jovicich et al., 2001).

Looking at the task from the shifting spatial attention prospective, the active-tracking tasks provides the participant to shift their attention to the moving balls as they track the target balls. In the passive task whilst tracking was not required there would still be an element of unprompted attentional shifts although it would be less than for the tasks that required tracking. Saccade planning is likely to be made in the passive tasks even if the saccades are not executed.

From the visual separation theory point of view, the presence of the fixation cross throughout the trials for both passive and tracking tasks created a fixed point in which the ten balls would move around, thus creating changes in visual separation between the fixation cross and the balls. Therefore, both the shifting attention and visual separation theories could makes sense of the results from the Jovicich et al., (2001) study.

Ohlendorf, Sprenger, Speck, Glauche, Haller & Kimmig, (2010) investigated brain activations associated with making smooth pursuit eye movements. They made comparisons between a static visual display with smooth pursuit eye movements that created retinal stimulus motion and times when the eye remained static and the stimulus moved creating retinal motion. In the third experimental condition the smooth pursuit eye movements and visual stimuli moved together in unison which nulled the retinal visual motion. They also varied the number of dots making up the visual stimulus. A rest condition consisted of a central fixation dot and then either 1, 4, 16 and 36 static background dots. The visual conditions again consisted of the static central dot, however, the background dots (1, 3, 16 and 36) moved laterally together in parallel; whereas in the visuo-oculomotor conditions the background dots stayed static, but the central fixation dot moved laterally. In the oculomotor condition the background dots moved laterally together with the fixation dot. Participants were asked to either attend to the central fixation dot or track its movement in the oculomotor and visuo-oculomotor tasks.

In the visual condition versus rest contrast, they found activation within the SPL (x24, y-54, z57) and in the visuo-oculomotor versus rest conditions, they also found activation in this area (x21, y-57 z54 and x-24, y-57, z54). However, there was no SPL activation for the oculomotor condition, which the authors classed as a notable result. They deemed this was likely due to the frame of reference (background dots) movement with the visual target (central dot). The visual separation hypothesis could more easily explain the results because of the visual separation that occurs when there is relative motion between the background and the visual target, where one remains static and the other moves. When there is no change in visual separation there is no activation in the SPL.

When looking at the results that Ohlendorf et al., (2010) found in light of the shifting spatial attention hypothesis, there were unlikely to be many spatial attention shifts because the dots in the study moved in a predictable and coherent manner, unlike in Jovicich et al., (2001) discussed above. Shifting requires movement that smooth pursuit does not produce and activation was not observed in the oculomotor task. In the tasks where activation within the SPL did occur, the visual and visuo-oculomotor tasks did not require any shifting of attention because the participants were required to fixate on the central fixation dot in the visual task or follow the movement of the central dot in the visuo-oculomotor task. This suggests that the shifting spatial attention theory is unlikely to be able to account for the activation that is seen in this study. However, we cannot definitely rule out the possibility that participants made more attention shifts in those experimental conditions where there was relative motion between the fixation dot and the other dots, and less in the condition where the background and fixation dot moved in tandem.

This stimuli in the Ohlendorf et al., (2010) study do, however, clearly show changes in visual separation. In the visual condition the central fixation dot remains static and the background dots move laterally thus creating a consistent change in visual separation between the fixation dot and the background dots which also creates a change in visual angle. The same principle applies in the visuo-oculomotor conditions where the background dots remain static and the central dot moves laterally. However, in the oculomotor task where the background dots and central dots move together laterally, the visual separation and visual angles remain the same and no significant activation was reported in the same SPL area. The visual separation theory is the most plausible alternative explanation to the one provided by the authors.

Jordan et al., (2001) investigated which areas of the brain were involved in mental rotation. They used three different types of stimuli for their study, to determine if the mental rotation of letters evoked a response in a different brain region compared to the rotation of abstract images. The three mental rotation tasks were: three-dimensional shapes as used by Shepard-Metzler in 1971 (cited in Jordan et al., 2001), letters, and abstract figures. Participants were given each stimulus in pairs on the screen and were asked to mentally rotate the object on the right so it matched the object seen on the left, they could then determine whether the image was the same or a mirror image. In addition, there were two control tasks, one comprising of determining if the nonrotated images were the same or different, and the other consisting of indicating which side (left or right) had a higher number of dots.

The results showed that the same subregion of the SPL activated for all rotation tasks versus baseline (rest condition). The authors concluded that for mental rotations to be successfully performed, changes to visual figures were required in a supramodal form, which may involve other modalities such as memory and attention (Jordan et al., 2001). It was argued that these processes take place in SPL.

The shifting spatial attention theory could be applied to explain the results of this study, the participant would need to shift attention between the imagined object and the original object it is to be compared too, therefore requiring a shift in attention and focus. When looking at these results from the point of view of the visual separation theory it is possible that mentally rotating the image and continuously comparing it to the original produces changes in visual separation between the elements that make up the stimuli. Whilst in other studies the visual stimuli involved a physical change in separation between objects that is observed by the participants; visual separation could also occur when the objects are imagined.

Peuskens, Sunaert, Dupont, Van Hecke, & Orban, (2001) investigated the neural basis of optic flow processing using a heading judgement task. Throughout the positron emission tomography (PET) and three fMRI experiments visual stimuli consisted of a ground plane that comprised of 50 white dots, an empty black sky and three static dots above the horizon. The central red dot was a fixation point with two peripheral red dots either side of the central fixation point. The 50 white dots that made up the group plane moved in a way that created a perception of forward motion that could be continuous or intermittent, with a focus of expansion (FOE) that could indicate current heading to the left or right of the central red fixation. In the *heading* task, participants were required to attend to the FOE that would shift location, whereas in a *dimming static* task, participants were required to identify the dimming of one of the peripheral dots. In the *dimming flow* task, the peripheral static dots (or, in another version the 50 white dots making up the flow field) would dim and the participant would identify the dimming via a button press.

Activation was observed in a heading minus all dimming static conditions contrast within the SPL (x16, y -70, z60[3]; and x-22, y-60, z60). Activation was also observed in the heading minus dimming flow conditions within the SPL (x18, y-69, z63; x24, y-60, z69 and x-21, y-63, z60). Peuskens et al., (2001) used their results to argue that the SPL and other activated regions are crucial for processing heading direction, visuospatial attention, and motor planning. However, it is plausible that the visual separation hypothesis could explain the activation that was observed within the SPL.

The participants were required to fixate to one object (the fixation point) but attend to other elements. The *heading* task consisted of a shifting element, the focus of expansion, and although the participants were not directly looking at the focus of expansion, they were expected to attend to it. Thus, they were attending to changing visual separation in the heading conditions, and not attending to it in the various dimming conditions. However, taking the perspective of the attention shifting theory it

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[3] Whilst Peuskens et al., (2001) reported using talaraich coordinates they used SPM96 software and since SPM96, MNI templates was used as standard (https://www.fil.ion.ucl.ac.uk/spm/software/spm96/) therefore it is likely that MNI coordinates system was used

is also possible to see the shifting of the FOE as driving shifts of spatial attention, while in the dimming task participants were attending with intent to detect an event at a fixed spatial location. Thus, these data could also provide evidence for the shifting of spatial attention as proposed by Vandenberghe et al., (2001).

It is also worth noting that the findings of Peuskens et al., (2001) regarding SPL appear to contradict those of Field et al., (2007) and Billington, Field et al., (2010), but this contradiction can be resolved by reconsidering the findings of all these studies in light of the visual separation theory. Peuskens et al., (2001) *heading judgement* condition, which did activate SPL, and the Field et al., (2007) *flow* condition which did not activate SPL are very similar to each other. The main difference between them is that the Field et al., (2007) condition did not include a fixation cross, instead allowing free eye movements. Introducing a static fixation point to an optic flow field introduces a relative motion (changing visual separation) signal, and this signal is probably the reason why the two experimental conditions produced different results in SPL.

Wolbers, Hegarty, Buchel, & Loomis, (2008) conducted experiments to investigate spatial updating using various numbers of geometric objects that were viewed against a ground plane made up of white dots. The participants would view the 1, 2, 3, or 4 geometric objects in either a *static* condition where the objects would disappear and after a delay phase the participants were required to indicate the location of one object, or in an *updating* condition, the participants would again see several geometric objects which would then disappear, and they would then observe simulated forward motion before being required to identify an objects location after taking into account the forward motion that had just occurred. During these conditions, the participants were required to encode the location and then retrieve this information after a delay. They found activation in the encoding phase within the same SPL area of interest (x-24, y-54, z52) which increased in relation to the number of objects on the screen. During the updating phase of spatial updating relative to the static condition delay phase, there was activation in the SPL at coordinates x-30, y-60, z44 and x32, y-60, z42 which also increased when there were more objects to update. Based on their findings, the authors argue that SPL performs spatial updating of the positions of objects that are out of our current field of view, e.g., the positions of objects are currently behind us relative to ourselves.

However, shifting of spatial attention was necessary when the participants observed the objects disappear and are then required to shift their gaze to identify the objects new location. The shifting spatial attention theory could account for the SPL activation that was observed in this study. During the encoding phase there was movement of the objects when they disappeared into the ground as well as the movement of the objects in relation to the white dots on the ground. During the crucial updating phase, the participant was internally simulating the motion in depth of several objects, which implies motion parallax between the objects. Such mental imagery involves visual separation changes and also potential for changes in the location of spatial attention, and so both theories we are considering can provide alternative explanation of Wolbers et al.,'s (2008) results.

Another study that specifically investigated the SPL was conducted by Wu, Wang, Zhang, Zheng, Zhang, Rong et al., (2016) where they investigated the function of SPL in relation to visuospatial attention. They used repetitive transcranial magnetic stimulation (rTMS) to temporarily produce the effect of a ‘lesion’ on the SPL. They began by using diffusion magnetic resonance imaging (MRI) to define the specific subregion of the SPL, the posterior part known as SPL5 as identified by a previous study (Wang, Yang, Fan, Xu, Li, Liu et al., 2015 - this study will be discussed later). The authors used a spatial attention task that had previously been used in another study Corbetta, Shulma, Miezin, & Petersen (1995) which consisted of four windows in what would be the four corners of an imaginary square and fixation cross in the centre of the screen. Each square consisted of 10 dots that were randomly chosen to either move in a left or right direction. The dots were either coloured red or orange that moved at either a fast or slow speed. Participants were required to identify target and non-target conditions via button presses. The target condition consisted of red dots that moved at a fast speed where all other conditions were classed as non-target. TMS was used on the identified subregion of the SPL on the left and right sides at coordinates x-20, y-70, z56 and x20, y-71, z50.

The authors reported that their results showed that the SPL was involved in the processing of visuospatial attention, and that the right SPL played a stronger role. This supports the findings of the Corbetta et al., (1995) study, which the authors replicated the visual stimuli from, who suggested that the more search that was required in a conjunction task the more shifting of attention was also required. With regards to the shifting spatial attention theory, in the target condition the participants were required to make a visual search for colour and motion to find the target condition and this involved shifting of spatial attention between the stimuli to achieve this. The results of this study can also be explained by the visual separation theory, where the fixation cross is key because it provides a static point that the moving dots change visual separation around. Changing visual separation can also be observed with the dots in the other windows when going at different speeds, making both the shifting spatial attention and visual separation hypotheses plausible explanations for the results of this study.

The eleven studies that were reviewed were either previously identified by Dr David Field's lab, or by literature search where the studies were identified on the basis that they had reported selective SPL activation, and their visual stimuli would be likely to generate activation according to both the shifting spatial attention hypothesis or visual separation hypothesis e.g. a fixed element and a moving element. Based on the studies that have been reviewed, the overall picture is that either of the two general hypotheses we have considered could potentially explain the results of the narrow studies that focus on specific task contexts; therefore, there is a need to perform empirical studies to adjudicate between these two theories. This brings us to identifying the main hypotheses and research question for this thesis.

1.4 Research question and main hypotheses

This thesis will investigate the nature of visual information processing in the SPL, primarily by critically testing the shifting spatial attention theory (Vandenberghe et al., 2001) and then testing the alternative visual separation theory. The shifting spatial attention hypothesis states that when an individual is required to shift their spatial attention during a task, activation in the SPL is expected. The visual separation hypothesis states that when an individual is required to attend to stimuli that depict a change in visual separation, activation will be observed within the SPL. It may be challenging to separate these two hypotheses because under most circumstances changes in visual separation have the potential to provoke spatial attention shifts.

Three fMRI experiments will aim to provide answers to these questions and explore the different hypotheses. The diverse claims made by previous studies regarding the function of this area highlights the importance of further understanding of this brain area's function

By replicating and extending the Vandenberghe et al., (2001) study design for investigating spatial attention shifting and then expanding upon it, we will be able to test the visual separation hypothesis as well as the shifting spatial attention hypothesis within the same experiment to determine which explains activation within the SPL area of interest. Once this question is established, more exploratory studies of SPL will make up the rest of this thesis.

1.5 Another alternative explanation of SPL functional specialism- divided attention

The world comprises of a large number of objects within any given scene and it would not be plausible for the visual system to attend to everything at once, therefore it becomes necessary for the visual system to select where attention should be placed within a scene and what information should be processed (McMains & Somers, 2004; Muller, Bartelt, Donner, Villringer, & Brandt, 2003). The goal-based attention mechanism suggests that attention is based on the individuals need to attend on a feature and the SPL has been observed to have been involved in goal-driven attention (Behrmann, Geng & Shomstein, 2004). The stimulus-driven attention mechanism often involves a fast response to the saliency of a stimulus requiring a shift of attention towards it to determine its importance (Connor, Egeth, & Yantis 2004).

In addition to these mechanisms, two theories of attention have become prominent. The zoom lens theory states that attention can be directed to a small area where the processing of information is likely to be fast and accurate or to a larger area which would process a number of stimuli, but this would ultimately reduce its efficiency (Muller et al., 2003). However, McMains & Somers, (2005) state that the zoom lens theory has two key pitfalls; interfering spatial locations and distractor stimuli are being needlessly attended to, even if they are task irrelevant. Whereas the multiple spotlight theory can dismiss interfering locations because it selects multiple locations that are spatially separate from each other (McMains & Somers, 2004).

The multiple spotlight theory suggest that attention can be distributed across multiple locations that are spatially separate allowing for multiple locations to be attended to, where (similar to the zoom lens theory) it has an element of decrease in processing efficiency as the size of location or number of locations to be attended increases (McMains & Somers, 2005). In the above discussion of previous brain imaging studies of SPL, wherever spatial attention shifting was raised as a possible explanation of patterns of brain activation, it would also be possible to invoke an explanation in terms of SPL becoming active whenever spatial attention is divided into multiple spotlights.

Therefore, the first experiment will be expanded to incorporate a test of the divided spatial attention hypothesis alongside the shifting spatial attention and visual separation hypotheses.

1.6 Secondary anatomical question – Wang et al., (2015)

A recent paper has proposed that the SPL can be parcellated into five distinct sections. Wang et al., (2015) describes the SPL as a mosaic, where there are distinct functions for the different areas. They used diffusion tensor imaging to provide information related to structural divisions within the SPL, as well as resting-state fMRI network analysis and co-activation patterns to determine the borders between these different regions within the SPL.

Using the Wang et al., (2015) parcellation as a map of the SPL we can add a secondary question to this thesis. Where does our region of interest fall within the parcellation map, does it fall within a distinct area as identified by Wang and colleagues? We can also use the studies reviewed above that have activation within the SPL and see if they also sit within defined areas of the parcellation or not. The results of the experiments conducted as part of this theses will also be compared with the SPL parcellation areas identified by Wang et al., (2015). Wang et al., (2015) also attribute functional specialisations to the five subregions they identify based on analysis of previous functional imaging papers. For example, they argue that SPL5 supports attention shifting based on the study of Vandenberghe et al., (2001) that is reviewed above. Our results will also be compared to the functions that they attribute to the different subregions.

1.7 Summary

The visual separation hypothesis proposes that the function of SPL is to represent the change in visual separation that occurs when an object changes location relative to another object within the retinal image. A shifting spatial attention hypothesis as proposed by Vandenberghe et al., (2001) will also be examined alongside a divided attention hypothesis to determine if the popular theory of attention is responsible for the activation observed in past studies of the superior parietal lobule. By investigating these three hypotheses and initially replicating the visual stimuli used in the Vandenberghe et al., (2001) study, the intention is to determine whether it is possible to accurately determine the function of this area of the SPL. The results of the first experiment highlighted some unexpected results produced by the way the stimuli were presented to the observer and therefore the second experiment focussed on explaining those unexpected results before a third experiment which break the visual separation hypothesis down further into two components: interobject distance and visual angle.

Chapter 2 - Experiment 1

2.1 Changing the focus of attention

Shifting spatial attention has already been highlighted in chapter 1 as a possible explanation for the selective activation that has been observed in the SPL across several studies of different behavioural tasks and cognitive functions. An alternative theory is the proposed visual separation theory can also be pitched as a plausible alternative explanation. Shifting spatial attention as a subset of the total set of attentional processes has been investigated using a range of neuroimaging techniques including fMRI, PET and TMS and multiple studies have identified activation within the SPL region of the brain which they have stated is related to the shifting of attention that occurred.

Shifting attention has been explored in numerous ways including: shifting of attention between locations (e.g. Capotosto, Tosoni, Spadone, Sestieri, Perrucci, Romani et al., 2013; Vandenberghe et al., 2001); shifting of feature-based attention, such as between colour and motion (e.g. Corbetta et al., 1995; Liu, Slotnick, Serences, & Yantis, 2003); and shifting of attention in relation to transient and sustained attention (e.g. Yantis, Schwarzbach, Serences, Carlson, Steinmetz, Pekar et al., 2002).

Corbetta et al., (1995) used PET to explore how attention and the parietal cortex were connected by investigating shifting feature-based attention between colour and motion. They used visual stimuli that consisted of four windows that contained several dots and a fixation cross in the centre of the screen. The task involved three conditions: a *colour* condition where the participants were required to identify a target (red-orange dots), over non-targets (orange dots); the *motion* condition where participants were required to identify the targets (fast speed), over non-targets (slow speed); and the *conjunction* task which required the participant to identify if there were red-orange dots at a fast speed (target), otherwise they were non-targets. Participants identified these targets and non-targets via a button press. In addition to the task conditions there were two control conditions, one where only the fixation point was visible on the screen, and another that comprised of two passive scans. The participants were not required to do anything with these search displays in the passive scans other than press the button keys alternately. The *passive* condition was contrasted with the active conditions to determine what activation, if any, was due to the task-related differences. The results showed that for the *conjunction* task there was distinct activation in the SPL and precuneus in the right hemisphere compared to the *colour* and *motion* conditions that only had low activation in the left hemisphere. This suggests that due to the increase in attentional load identifying two elements in a search task rather than the single element in either the *colour* or *motion* conditions, that attention was divided. This is a theme we will return to.

Another study using colour and motion to investigate shifting of attention was conducted by Liu et al., (2003) who used rapid serial visual presentation (RSVP) to present coloured dots to the participants. The dots would move in one direction and once per second would change colour and movement direction. Participants were required to attend to either colour changes or motion direction at any point during the task, where sustained attention would occur when one colour type (e.g. green) and motion type (e.g., lower-left motion) were displayed (*hold* conditions); or shift attention when the other colour type (e.g., red) and motion type (e.g., upper-right motion) was displayed (*shift* conditions). The fixation cross was in the centre of the screen throughout the trials. When subtracting the sustain attention tasks – *hold colour* from *hold motion*, the authors found bilateral activation in the SPL, the inferior parietal lobe, the precentral gyrus, and middle/inferior temporal gyrus which was observed in motion compared to colour. The change in movement of the dots in the sustained attention condition produced a higher BOLD signal in the SPL compared to the feature-based change in the colour of the dots suggesting that when attention is sustained the SPL cares more about the spatial properties than feature-based properties.

A fMRI study conducted by Yantis et al., (2002) investigated shifting of spatial attention also used RSVP but this time incorporating letters and required participants to identify numbers within the letters being presented. There was a fixation square in the centre of the screen with the letters situated to the left and right of the fixation square and the participants were required to identify the digit via a button press. A tick which would appear either on the left or right of the midline informed the participants where to attend. Within the letter strings, the participants indicated the numbers they were searching for, a '3' indicated that they should sustain attention at their present location whereas '7' indicated that the participant should shift attention to the other target location. Their results showed that the SPL had a high BOLD signal for the contrast of shifting attention versus sustained attention events, and thus are consistent with the theory that SPL has a specific role in shifting attention.

Capotosto et al., (2013) used gabor patches to investigate shifting of attention and different locations. They used repetitive TMS (rTMS) to provide interference to the SPL to determine the effect of inhibition to that brain area when shifting of attention occurs. The visual stimuli consisted of two drifting gabor patches that were situated on either side (left or right) of a central fixation cross. The participants were required to identify a change in the orientation of movement of the gabor patches and indicate this via a button press. The gabor patches would also change colour to indicate to the participant which location they should be attending to whilst fixating on the fixation cross. The results showed that for shift cues compared to stay cues the medial SPL (mSPL) showed fMRI activation (average activation x12, y-70, z62 MNI[4]). The TMS produced interference to the task performance in the mSPL after shifts of attention, which were independent of the shift direction. Whereas task performance for the ventral intraparietal sulcus (vIPS) was impaired contralaterally, when TMS was performed, independent of whether there was a shift or not. This paper presents some convincing evidence in favour of attention shifting functions of the mSPL, however, whether the region that is targeted in this paper is the same as the one we are focusing on or whether it is more medial is open to question.

Vandenberghe et al., (2001) also investigated shifting of attention to different locations using fMRI and target squares that moved laterally across the midline of the screen. This time the participant was required to identify a dimming event that would occur in the target square via a button press. A fixation cross also stayed on the screen throughout the trials. Vandenberghe et al., (2001) interpreted their findings as

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[4] To keep all coordinates within the thesis as MNI coordinates, those studies that reported talaraich coordinates were converted to MNI coordinates. We used MNI<->TAL (Yale University BioImage Suite Web 1.0.0., 2018 to achieve this.

showing support for the attention shifting account of SPL function. This study will be discussed in more detail later.

Each of the above studies were investigating changing focus of attention and used a variety of visual stimuli to complete this investigation which ranged from utilizing shapes, letters, and numbers to abstract gratings. Shifting attention was explored several ways such as feature-based, shifting attention across locations and transient and sustained attention. What linked these studies was some form of movement within the visual stimuli used in the tasks. A constant feature across all these studies was a fixation point (predominantly a cross but a square was also used in one study). These fixation points were included to ensure that the participants had somewhere to fixate to enable their eyes to remain still which ensured that the retinotopic locations of the stimuli were as the experimenters intended while covertly attending to other features that were presented on the screen.

Fixation points are added to visual stimuli to keep the eye focussed and achieve retinal locations that are fixed on the visual stimuli whilst it is being viewed. However, this may not be the only effect that the addition of the fixation points has. Our proposed visual separation theory sees fixation points as a fixed-point relative to which other objects' movements are perceived. This results in salient percepts being added to the experimental stimuli such as the distance between two points, the expansion or contraction of that distance and relative motion. This makes the visual separation hypothesis a plausible alternative explanation to the shifting attention hypothesis in many experimental paradigms, even when there are different specifics of shifting attention being investigated. We therefore investigated the shifting of attention hypothesis alongside the visual separation hypothesis in this first experiment of the thesis. We replicated and extended the Vandenberghe et al., (2001) study because the paradigm could be modified to pit the shifting attention and visual separation hypotheses against each other within the same experiment.

2.2 Vandenberghe et al., (2001)– paradigm for studying attention

The first experiment of this thesis will initially replicate the Vandenberghe et al., (2001) study using the same type of visual stimuli and follow the methodological constraints it abided by. The visual stimuli in the first experiment conducted by Vandenberghe et al., (2001) comprised of a white fixation cross (0.27°) and white target square (0.44 x 0.44°) on a black screen (see Figure 2.2.1.). The target square would be displaced throughout the trials between one of ten pre-determined locations across the midline of the screen (see Figure 2.2.2.). Note that the target square did not move smoothly, it disappeared and reappeared at the new location, which we will refer to as displacement. Null events were included, in which the target square would remain at the same location as the previous target square for one more period before moving on to the next location (see Figure 2.2.1.b and 2.2.1.c). Each run consisted of 96 events and 48 null events producing 144 events in total. Each event had an onset asynchrony of 2260 ms, which is the time that it takes from the beginning of one event to the beginning of the next event. During a run, the 96 events last 216.96 sec in total and the null events 108.48 sec creating an overall run duration of 325.44 seconds.

The path of the target square was considered carefully by Vandenberghe and colleagues. The ten pre-determined locations across the midline of the screen were spaced equally across the left- and right-hand side of the screen from the midpoint.

Within a run, half the shifts were leftward, and half of the shifts were rightward. Within each of these two shift direction types, one third began and ended to the left of the fixation cross, one third began and ended to the right of the fixation cross, and one third crossed the midline. This planning ensured that there was not any bias towards attending to any specific spatial location across the different locations.

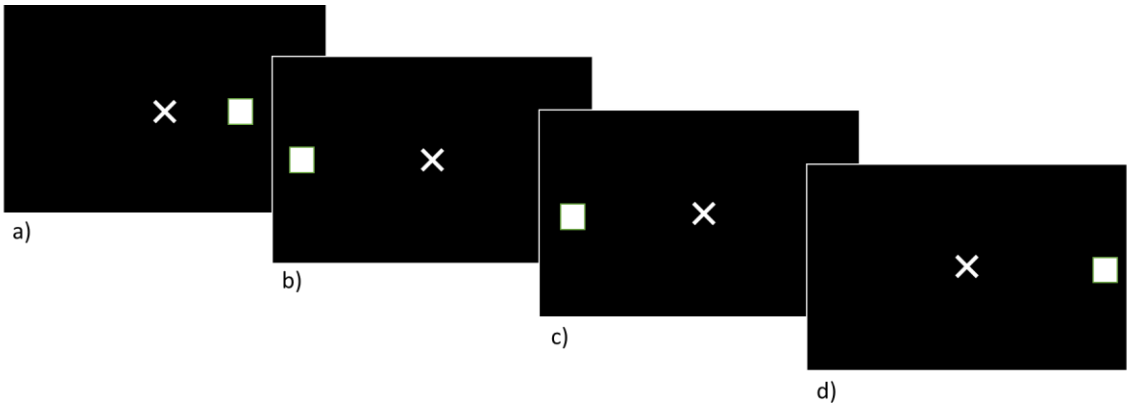

Figure 2.2.1. Vandenberghe et al., (2001) visual stimuli where a) shows the fixation cross in the centre of the screen and the target square in one of the ten pre-determined locations across the midline of the screen; a shift event moves the target to one of the other predetermined target locations shown in b) and c) depicts a null event where the target square stayed in the same location for two successive periods; and d) shows the target square displace to an alternative location after the null event.

To maintain a roughly constant level of attention throughout the run including during the null events, participants in the Vandenberghe et al., (2001) study were asked to identify dimming events whilst focussing on either the fixation cross (covert attention) or using saccades to track the target square (overt attention). These two types of attention were separated into two different runs of the experiment. The dimming event could occur in the target square only and 24 dimming events were distributed through each 325.44 sec run. Each dimming event lasted 100ms and could occur at any point during the 96 events and 48 null events within each run. Because the dimming event could occur unpredictably at any point in time it required sustained attention from the participant to accurately indicate when a dimming event had transpired. This meant that during the null events the participant would also be required to sustain attention rather than become inattentive. The null events would therefore be the main subtraction condition for detecting activation in brain areas that are more active in shifting attention than sustaining it. The participants were required to identify the dimming event using a button box and were able to detect 75% of the covert dimming events and 83% of the overt dimming events making the dimming events suitably demanding to ensure sustained attention from the participants.

The results of the study showed strong bilateral activation at MNI[5] coordinates x-24, y-61, z63; x-33, y-58, z63 and x14, y-68, z57; x26, y-62, z68. This is within the SPL brain area and extended to the IPS which the authors identified as the Superior Parietal Gyrus and argued was due to the shifting spatial attention to follow the target square because, relative to sustaining attention, activation was observed at those coordinates in both covert and overt trials. Impressively, this was the only brain region that was active in a conjunction analysis of covert shifting minus sustaining and overt shifting minus sustaining. However, as argued in Chapter 1, these results could also be explained if SPL was specialized for detecting and encoding visual separation and changes in visual separation.

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[5] Whilst Vandenberghe et al., (2001) reported using talaraich coordinates they used SPM99 software and since SPM96, MNI templates was used as standard (https://www.fil.ion.ucl.ac.uk/spm/software/spm96/) therefore it is likely that MNI coordinates system was used.

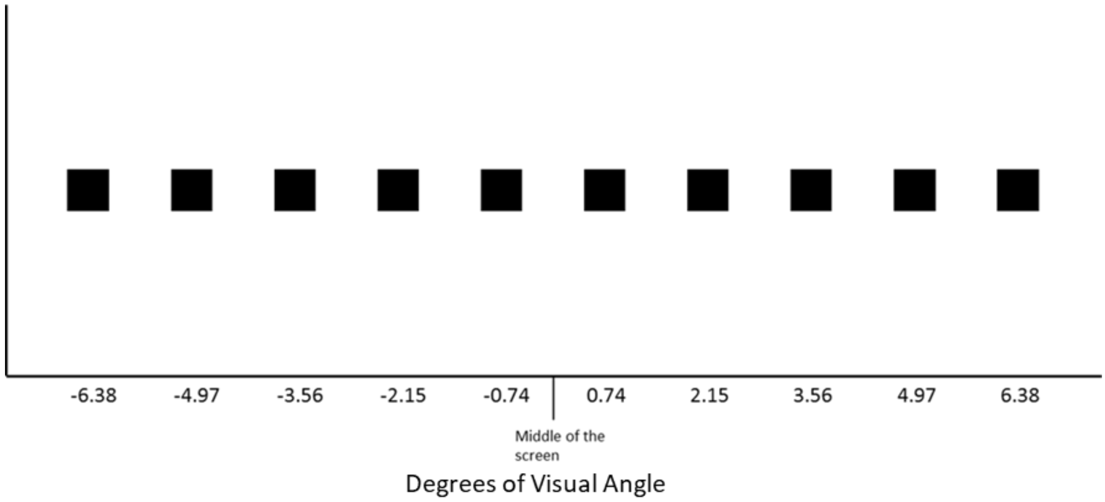


Figure 2.2.2. The ten pre-determined locations across the midline of the screen which was used within experiment one from the Vandenberghe et al. (2001) study (0.74, 2.15, 3.56, 4.97 and 6.38° on either side of the centre)

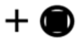
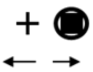
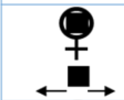
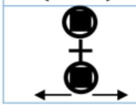
2.3 Hypotheses and predictions

As previously mentioned in Chapter 1, an additional hypothesis will be investigated alongside the shifting spatial attention hypothesis and the visual separation hypothesis. The divided attention hypothesis is a variant of spatial attention which states that the function of the SPL is related to dividing attention between multiple spatial locations. The visual stimuli used to create and manipulate conditions of divided attention will be explained below.

To pit the shifting spatial attention hypothesis against the visual separation hypothesis we expanded the Vandenberghe et al., (2001) paradigm to include a condition that kept the shifting attention elements but removed visual separation. This was achieved by omitting the fixation cross and did not interfere with the behavioural task because the fixation point is irrelevant when making saccades to track the displacing target. There is no visual separation under these conditions because a solitary object, in this case the target square, displaces but does not produce visual separation on its own, therefore no significant activation is expected in the SPL. However, the shifting spatial attention hypothesis predicts activation in the SPL due to the displacement observed in this condition compared to sustained baseline. Whenever a saccade is executed, attention is briefly disengaged from its current location before shifting to the new location. In a seminal paper Deubel & Schneider, (1996) showed that shifting visual attention in this way is a mandatory part of the process of planning and executing a saccade.

If the *shifting* condition without a fixation cross does not activate the SPL and therefore supports the visual separation hypothesis, then committed attention theorists could argue that the SPL acts to divide rather than shift attention e.g., (Jans, Peters, & De Weerd, 2010; McMains & Somers, 2005). Although, when a solitary square stimulus displaces there is no division in attention whereas there would be if there was a displacing square stimulus and fixation cross present. This would make sense of results where activation was present in all but the single displacing square condition. In order to rule this out we further added two conditions that kept some of the constraints of the Vandenberghe et al., (2001) study: the 10 pre-determined locations, size of the visual stimuli, null events and dimming event. The two additional conditions consisted of three main elements, two squares above and below a fixation cross that displaced in unison. A cueing circle(s) were also added to inform the participant where the dimming event will occur. Visual separation remains constant between these three elements and therefore no significant activation was expected under the visual separation hypothesis whereas in the Vandenberghe et al., (2001) study the separation varied because the square displaced across the screen whilst the fixation cross remained static throughout. To introduce division of attention, participants were required to identify a dimming event that would occur in the upper or lower squares whilst fixating on the fixation cross. If the SPL is responsible for divided attention, then positive activation is expected for this condition where divided attention took place. The various predictions made here are summarized in relation to the visual stimuli in Table 2.3.1.

Table 2.3.1. Hypothesis grid showing expected activation (✓) in experimental conditions for each hypothesis to be investigated. The absence of a tick indicates that indicates that activation is not expected. The double ✓ for condition 7 in the divided attention column depict a stronger activation for condition 7 than the other conditions. The conditions consist of a target square(s) and fixation cross, as well as an identification circle to inform the participants where to look. The arrows depict presence of displacement to one of the ten pre-determined locations across the midline. Absence of arrows are static stimulus conditions.

Condition	Number	Shifting Spatial Attention	Visual Separation	Divided Attention
	1	✓		
	2			
	3	✓	✓	✓
	4			
	5	✓	✓	✓
	6	✓		✓
	7	✓		✓ ✓

2.4 fMRI contrasts

The conditions where we expect activation within the SPL under the visual separation hypothesis are those where the fixation cross remains static and the target square displaces laterally across the midline of the screen. This creates the perception of changing visual separation between two objects as the target stimuli moves to different locations the visual separation and visual angle also changes. We would not expect there to be any detectable activation in an fMRI block design under conditions when the fixation cross and target square remain static because the visual separation and visual angle between these objects does not change throughout that block, and so any initial visual separation related activity at the start of the block will be reduced by neural adaptation. Each of the experimental conditions was contrasted with the baseline which consisted of a static target square (with dimming events). Additional contrasts will also be conducted between conditions containing changes in perceived visual separation and the novel experimental condition of a single displacing target square without a fixation cross.

2.5 Method

2.5.1 Participants

19 participants were recruited via advertisements at University of Reading. There were 16 females (3 males) with a mean age of 22.8 years (age range 18 years - 37 years). Ethical approval from the University Research Ethics Committee (UREC 14.29) was obtained and written informed consent was acquired from the participants prior to scanning. The fMRI scans were performed following the University of Reading's Centre for Neuroscience and Neurodynamics (CINN) guidelines and

protocols for scanning participants. Unfortunately, we had to exclude one participant from experiment 1 and one participant from the localiser due to technical issues with the 4D functional data. A power analysis using (Mumford & Nichols, 2008) method and conducted on fmripower software (fmripower.org) determined that with the threshold set at 0.05, 20 participants would provide 99% power to detect an effect of 1.30 standard deviation units in both hemispheres of the SPL. This would still provide reasonable power if one or two participants were excluded from analysis.

2.5.2 Functional localisers

Localiser scans were used in each of the three experiments of this thesis to locate the region of interest in the SPL. Originally in experiment 1 we had two kinds of localiser conditions that were used; however, one kind was quickly assessed to be unsuitable for activating the SPL and was discounted from further analysis. The successful localiser replicated existing visual stimuli from previous studies (reported in Chapter 1) who had successfully identified activation within the SPL region of interest. In the first experiment the localiser comprised of four conditions. Condition 1) an *eye movement localiser* (*EML*) that consisted of a black background with a single white dot that would move around the screen in any direction and displacement length. Participants were required to follow the white dot wherever it displaced. 2) *flow* - a textured ground plane/blue sky condition with forward motion trajectory (Field et al., 2007); 3) *poles* - a textured ground plane/blue sky condition with the addition of green poles that would appear with only two poles on the screen at any one time (Inman, 2014b); 4) *road* - a textured ground plane/blue sky condition with the addition of parallel white road edges that weaved along simulating the forward motion trajectory (Field et al., 2007);– see Figure 2.5.1. In these three conditions participants were asked to move a joystick to indicate their heading direction in correspondence to the motion they were seeing on the screen.

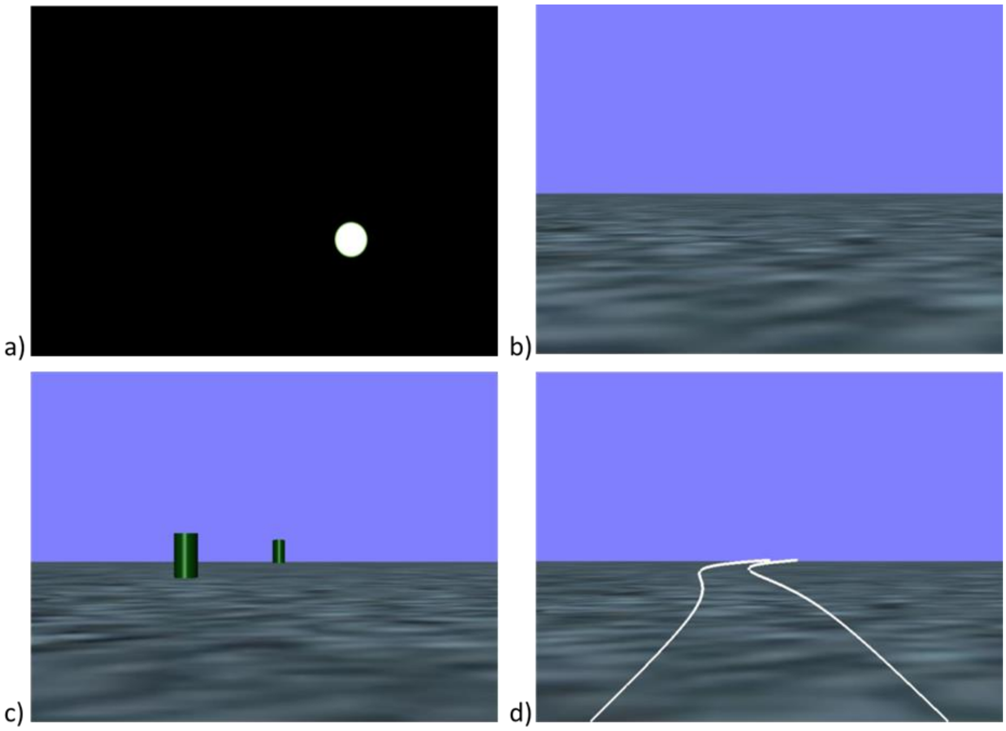


Figure 2.5.1. Conditions used in experiment 1 where (a) the *eye movement localiser* that consisted of a black screen and white dot (*EML*); (b) is the *flow* condition consisting of the textured ground plane and solid blue sky (*flow*); (c) same as *flow* but with the addition of green cylinders (*poles*); and (d) same as *flow* but with added road edges (*road*) (pictures taken from Inman (2014)

The visual stimuli for the localiser experiments were created using Vizard 3.0 (WorldViz). Participants were pre-taught the task prior to scanning to ensure they understood how the heading task worked and how to use the joystick to indicate their heading direction that was required for the localisers in all experiments. For this localiser we used a block design comprising of 36 blocks with each of the four conditions repeated 6 times. The *rest* block (blank ground plane and grey sky plane) was repeated 12 times, and there was a red or blue indicator screen that was presented prior to either the *EML* (blue screen) or *flow*, *road,* or *poles* conditions (red screen) that would inform the participant whether they needed to use the joystick or could just follow the stimulus with their eyes. Each block lasts 16 seconds and the additional coloured screens that indicated what the participant was expected to do lasted 1 second which made the overall experiment 600 seconds long. The *flow* and *road* conditions had a 'flipped' path in half of their blocks where the path weaving and winding directions would be flipped to reduce any predictability.

Whilst these conditions were investigating other theories in the previous studies, the activation in SPL that was observed could be attributed to the changes to visual separation. In the *road* condition (Field et al., 2007) the road edges weave and wind along the ground plane in a forward trajectory creating a change in visual separation due to the converging lines of the winding road (see Figure 2.5.2.). Another condition that was a high activator in the SPL was in the Inman, (2014) study where two green poles would appear, one in the background and one in the foreground. The appearing and disappearing of these poles combined with the forward motion trajectory provides changes in visual separation between the poles. The *flow* condition was the subtractive baseline in the localiser scan. The *eye movement localiser* was included as a condition to exclude all voxels that were involved in making saccades from the localised regions. This was done to ensure that the *eye movement localiser* was not just isolating neural correlates of differences in eye movement planning or execution invoked by the different stimuli.

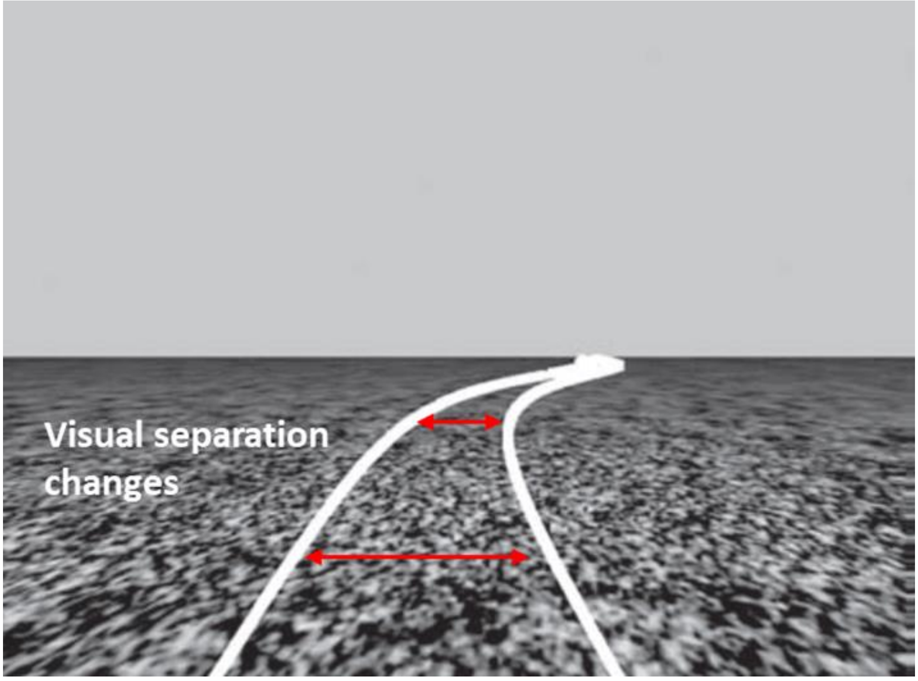


Figure 2.5.2. Still image taken from the Field et al. (2007) study of the *road* condition where the road edges change in visual separation as the 2D projection of the road moves and bends in shape due to simulated forward winding trajectory

2.5.3 Experimental Stimuli and Design

This experiment comprised of 7 experimental conditions where the visual stimuli consisted of a fixation cross, target square(s) and a circle that cued the participant about the behavioural task. Unlike Vandenburghe, we used a block design, but to maintain full comparability with Vandenburghe within the blocks the timing of stimulus shifts were jittered in the same way that the Vandenberghe et al., (2001) experiment did, producing null events. These null events would keep the target square in the same location for double the normal amount of time. The baseline blocks in our experiment consisted of a single static square and the dimming events could occur across all conditions including the baseline, this ensured that attention was sustained at all times. Including the baseline there were 49 blocks, made up of 6 repeats of each block type, except baseline, which occurred 7 times. Each block lasted 18 seconds and the experiment was preceded by a black screen that faded up to show the target stimuli and indicated the experiment had begun. The duration of the experiment was 882 seconds.

The experimental stimuli were written in Matlab (Mathworks, Inc.) using Psychtoolbox (Brainard, 1997; Kleiner, Brainard, & Pelli., 2007; Pelli, 1997) and as already mentioned consisted of a fixation cross, target square(s), and a cueing circle that would let the participants know whether to attend to the fixation cross (covert attention) or the target squares (overt attention with eye movements). The two types of attention were used by Vandenberghe et al., (2001) and both are included in this experiment. Where our stimuli differ from the Vandenberghe et al., (2001) study, however, is the addition of a cueing circle to instruct the participant whether to deploy covert or overt attention. The Vandenberghe et al., (2001) study informed their participants in half of the runs to attend to the target square and in the other half of the runs to attend to the fixation cross, which they then counterbalanced across the participants. The cueing circle in our experiment allowed the comparison of overt and covert attention within a run rather than having two runs; this is a more efficient fMRI design (Henson, 2007). Out of the eight conditions, six contained a single target square including multiple visual elements (see Table 2.5.3.). Condition 3 and 5 were replications from the Vandenberghe et al., (2001) study requiring covert attention (condition 3) and overt attention (condition 5). Conditions 2 and 4 take away the displacements from conditions 3 and 5 but continue the need for covert and overt attention.

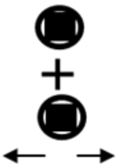
Table 2.5.3. First five conditions where the identification circle informs the participant where to look, either the fixation cross (covert attention) or target square (overt attention). Arrows depict lateral displacements across the midline to one of the ten pre-determined locations.

Condition	Number	Description
■	0	Single static square
■ ← →	1	Single target square moving laterally
⊕ ■	2	Covert attention, static target square
⊕ ■ ← →	3	Covert attention, target square moving laterally
+ ●	4	Overt attention, static target square
+ ● ← →	5	Overt attention, target square moving laterally

Condition 1 is the key condition for pitting the shifting spatial attention and visual separation hypotheses against each other. Under the shifting spatial attention hypothesis activation within the SPL is expected because the target square is still displacing to one of the ten pre-determined locations resulting in attention shifts (Deubel & Schneider, 1996). However, from the vantage point of the visual separation hypothesis the single target square without the fixation cross eliminates any changes in perceived visual separation because there is only one object and two or more are needed to create a visual separation between them, and therefore no significant activation within the SPL is expected.

To investigate the divided attention hypothesis the final two conditions were created and featured two targets squares alongside the fixation cross. In these conditions the fixation cross would displace with the target squares to one of the ten pre-determined locations, in unison. The identification circle in conditions 6 and 7 would instruct the participants where the dimming event would occur, in the upper square only (as in condition 6) or either the upper or lower square (as in condition 7). Participants were required to fixate on the fixation cross for these two conditions but attend to either the upper square or the upper and lower square and identify the dimming event via a button press (see Table 2.5.4.).

Table 2.5.4. Expanding the Vandenberghe et al., (2001) study to include conditions that require the participant to divide their attention to two or more locations. In these conditions the participants are required to look at the fixation cross throughout the trials and the identification circle informs the participants where the dimming event will occur. Either the upper square only in condition 6 or either the upper or lower squares in condition 7.

Condition	Number	Description
	6	Two squares and fixation cross moving laterally together
	7	Two squares and fixation cross moving laterally together

Null events were also used within all blocks of this study in order to maintain direct comparability of the results with those of Vandenberghe, and these would consist of the square remaining in the previous position (as in Vandenberghe et al., 2001 study) and would occur randomly throughout the trials ensuring that they would be unique for each participant. The baseline block that was not modelled explicitly in the design matrix consisted of a single static square, on which the participant fixated gaze for the duration of the block. Dimming occurred in the baseline with the same frequency as in the other block types.

The fixation cross (horizontal and vertical size = 0.27° and luminance = 0.06 cd/m^2) remained static in the midpoint of the screen for conditions 2 to 5, but would displace with the target squares in conditions 6 and 7. The target square was a single square (size = 0.66° x 0.66°^{2} and luminance = 0.06 cd/m^2) and would displace horizontally between 10 pre-determined locations (-6.38, -4.97, -3.56, -2.15, -0.74, 0.74, 2.15, 3.56, 4.97, 6.38°) relative to the middle of the screen in conditions 1, 3, and 5[6]. In conditions 6 and 7 the fixation cross was situated between the two target squares vertically and would also displace simultaneously to the 10 pre-determined locations.

The low luminance level of the visual stimuli was chosen partly to avoid a starburst pattern visual effect that occurred for each visual stimulus displayed against a dark background where the display device was at higher luminance levels. The low luminance level also ensured that the screen edges were not visible to the participants when the lights in the scanning room were switched off. This removed any additional visual information on the screen for the participants allowing them to be fully immersed in the visual stimuli without a more obvious figure and ground

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[6] The target square displacement relates to the removal of the target square from one of the ten pre-determined positions on frame N to be re-drawn at its new location (another already identified pre-determined location) on frame N+1.

representation. This was especially important in our critical condition (single square displacing) as it prevented the perception of changing visual separation between the isolated stimulus and the screen edges. This precaution was also taken by (Ohlendorf et al., 2010) but not by the other studies described in this thesis.

The dimming events were configured to ensure that they were fairly salient to the participant and it was determined that a ‘blinking’ rather than smoothed ‘dimming’ was necessary due to the low level of luminance of the undimmed stimuli being close to the minimum possible for the display device (dimming event luminance = 0.01 cd/m^2). During piloting, we found that gradual dimming of the target square was too subtle and easily missed whereas the blinking event ensured that the participant was able to attend to the target square in both the overt and covert conditions to identify the ‘dimming event’ and record this on the button box with approximately 80-90% success rate.

2.5.4 Procedure

Participants were pre-taught both the localiser and experimental tasks, before entering the scanner to ensure that they understood the nature of each task and that they were required to use the joystick for the most of the localiser conditions and for the experimental task to identify a dimming event by using a button box. The purpose of the cueing circles in the first five conditions in the experimental task (where the participant should attend) and the last two conditions (where the dimming event will occur) was also explained to the participant.

Upon completion of the practice tasks and once written informed consent was provided and the participant was deemed suitable for scanning, they were asked to lie down on the scanner bed. A 12-channel head coil was positioned around the participants head and the viewing goggles (Nordic Goggles - http://www.nordicneurolab.com) were attached and positioned. The goggles were used as the source of delivery of the visual stimuli throughout this study. An eye patch was put over the participants right eye to allow viewing from the left eye only, this was done to avoid the binocular diplopia that the Nordic goggles produce in many participants. Diplopia needed to be avoided in our experiment because it would create changes in perceived visual separation particularly in condition 1 where it was essential to avoid them. The goggles were positioned a few millimetres away from the eye to ensure comfortable viewing by the participant. This distance varied slightly between participants to take into consideration the different face and eye shape and eyelash length to ensure a comfortable viewing experience that did not distract from the task. The goggles were adjusted to ensure that the participant could focus clearly on the visual stimuli on the screen. This removed the need to wear glasses or contact lenses for those participants who would do so normally.

The joystick was attached to a piece of cardboard that the participant would lie upon to ensure the correct position by the right side of the participant to allow them to easily reach down to use the joystick during the localiser task. The button box consisted of four buttons, and any button could be used to respond which eliminated the need for the participant to remember which button to press whilst lying in the scanner. The button box was given to the participant as well as an alarm bell in case they needed to be removed quickly from the scanner. Once the participant was placed in the correct position in the scanner, the lights were switched off and the participant was spoken to via an intercom by the researcher.

Once the above procedures were complete scanning commenced with the main experiment being presented before the localisers. Participants were reminded of the instructions prior to the start of each experiment (experiment 1 and localisers) via the intercom to ensure that they were fully aware of what was required of them throughout the task.

2.5.5 fMRI Data Acquisition

Imaging data was acquired using a SIEMENS MAGNETOM Trio 3T MRI scanner located at the Centre of Integrative Neuroscience and Neurodynamics (CINN) at the University of Reading. Other equipment used in this experiment were the Nordic Goggles (http://www.nordicneurolab.com) which were mounted onto the head coil, an MRI compatible button box that had 4 coloured buttons and the Magstim MRI compatible joystick. Due to the nature of the behavioural task any button could be pressed on the button box to record a response.

A 28 second auto alignment localiser scan was performed first with the repetition time (TR) 3.15ms and the echo time (TE) 1.37ms. The flip angle (FA) was 8 degrees, and the voxel size are 1.6 x 1.6 x 1.6mm with 128 sagittal slices per slab at a thickness of 1.6mm. The T1 anatomical scan lasting 4.34 minutes was performed next where the TR = 2020ms, the TE = 2.52ms, and the FA = 9 degrees. 176 1mm thick sagittal slices were acquired with a matrix size of 256 x 256, and a FOV of 250mm. This resulted in 1 x 1 x 1mm isotropic voxels. A field map was also acquired to help undistort the images acquired for the EPI (Echo Planar Imaging). The voxel size was 3.0 x 3.0 x 3.0mm and there were 36 axial slices with a TR = 400ms and TE1 = 5.19ms and a TE2 = 7.65ms.

The main EPI scan for this experiment was 15.09 minutes duration and was next to be performed. The TE = 30.0ms, the flip angle was 90° with a matrix size of 128 x 128 and a field of view (FOV) of 256mm. There were 63 axial slices obtained with interleaved slicing, no interslice gap and a thickness of 2.00mm. The TR = 1500ms and the number of volumes that were acquired was 595 with a voxel size of 2.0 x 2.0 x 2.0mm.

A second field map was performed after the main scan with the same parameters already described. The localiser that was used in the analysis was 10.33 minutes in duration and had a TR = 1500ms, TE = 30.0ms, and a FA = 90°, a matrix size of 128 x 128 and a FOV of 256mm. There were 63 axial slices that were interleaved with no interslice gap and a thickness of 2.00mm and 413 volumes were acquired with a voxel size of 2.0 x 2.0 x 2.0mm. A final field map was then acquired, again with the same parameters already mentioned.

2.5.6 fMRI Data Analysis

2.5.6.1 First Level Analysis

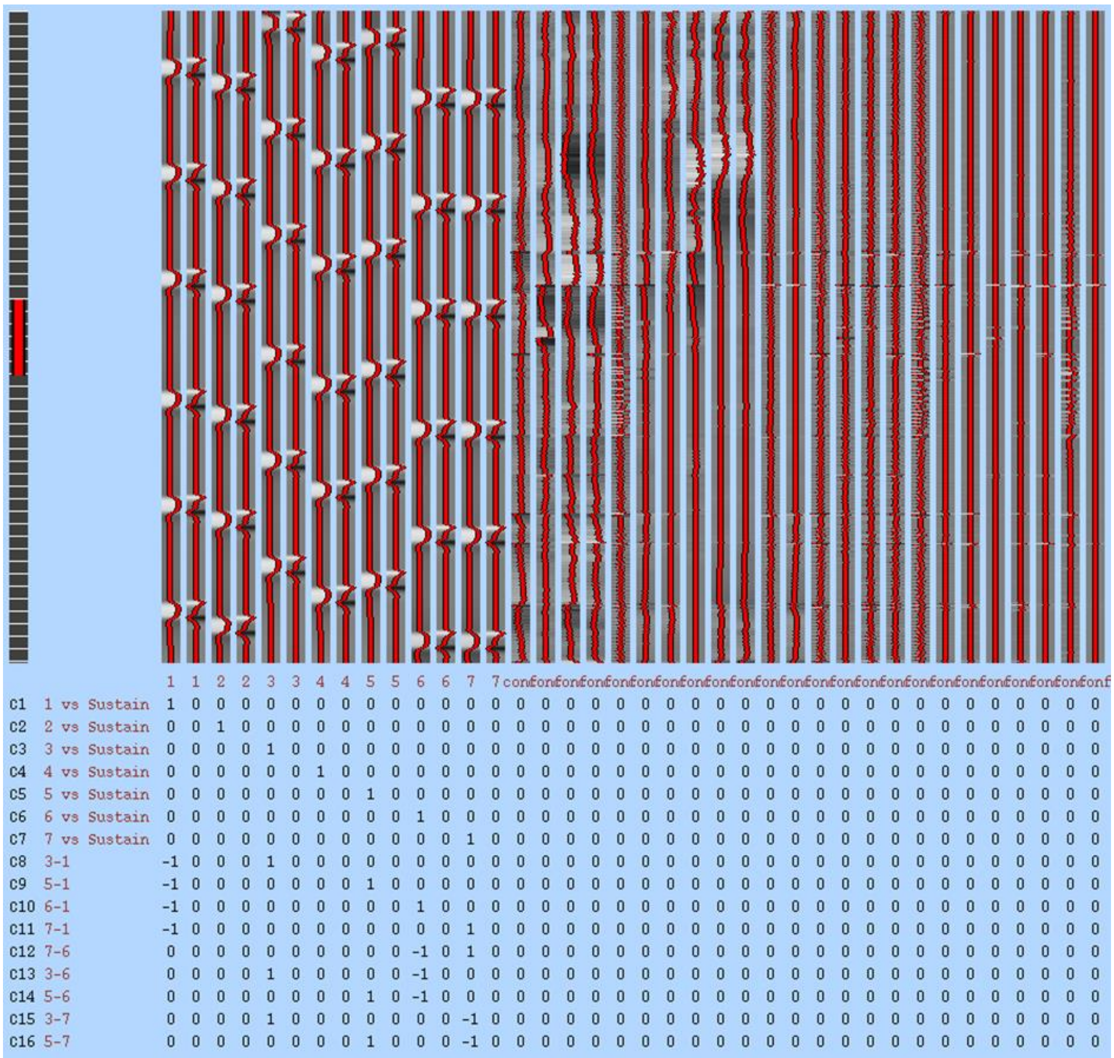
The fMRI data processing for this was experiment was carried out using FSL (FMRIB's Software Library) version 5.0.9. Pre-processing as well as general linear model (GLM) fitting for first level and group analysis was carried out using FEAT (FMRIB Expert Analysis Tool) (Woolrich, Behrens, Beckman, Jenkinson & Smith., 2004; Woolrich, Ripley, Brady, & Smith, 2001). At first level analysis, a number of pre statistics steps were applied, they were as follows: motion correction using MCFLIRT (Jenkinson, Bannister, Brady & Smith, 2002; Jenkinson & Smith, 2001); interleaved sliced timing correction; brain extraction tool (BET) (Smith, 2002) to remove any nonbrain material from the scan; spatial smoothing with a FWHM of 5mm and a high pass filter set at 90 sec across all individuals. Registration was to standard space MNI template.

We chose to enter the standard plus extended motion parameters of the GLM, which include the volterra expansion of the 6 standard motion parameters based on the study of Lund, Nørgaard, Rostrup, Rowe & Paulson., (2005). Lund et al., argued that residual motion could significantly impact the validity of activation and by including a volterra expansion rather than continuing with the standard 6 motion parameters, the inter-session variability is significantly reduced. Lund et al., (2005) reported results showing that the activation which remained after the residual motion had been modelled was more clear and focused activation, which they assert provides stronger validity on the remaining activation. We also used fieldmaps to tackle any inhomogeneity found in the magnetic field that could subsequently create distortions to the images (Togo, Rokicki, Yoshinaga, Hisatsune, Matsuda, Haga et al., 2017).

The general linear model (GLM) was used to perform the analysis on each voxel, and in addition to this, temporal derivatives were also added with a high pass filter of 90 seconds. Explanatory variables (EV) were used to model the timecourse of each for the seven experimental conditions, although the baseline condition was not explicitly modelled as a separate regressor. The design matrix also shows the Volterra expansion of the estimated head motion parameters (see Figure 2.5.5.) where time is shown running top to bottom.

2.5.7 Contrast analysis in FEAT

The first level contrasts that were implemented in FEAT (Woolrich, Ripley et al., 2001) comprised of the 7 conditions versus baseline (static square) and several contrasts to further test the predictions. The key condition for the shifting spatial attention hypothesis was condition 1 (single square displacing) where activation would be expected, however for the visual separation hypothesis no significant activation is predicted. Other key contrasts were for conditions 3 – 1 (fixation cross, cueing circle and displacing single square viewed covertly – single displacing square) and 5-1 (fixation cross, cueing circle and displacing single square viewed overtly – single displacing square) that were expected to activate the SPL region under both the shifting spatial attention hypothesis and visual separation hypothesis. Also, condition 6-1 (fixation cross, two squares, cuing circle in upper square, displacing in unison – single displacing square) and 7-1 (fixation cross, two squares, cueing circle in upper and lower squares, displacing in unison – single displacing square). Both the visual separation hypothesis and attention shifting predicted no SPL activation in these contrasts. Additional contrasts were added to explore other potentially interesting effects (see design matrix in Figure 2.5.5).



		1	1	2	2	3	3	4	4	5	5	6	6	7	7	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf	conf
C1	1 vs Sustain	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	2 vs Sustain	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C3	3 vs Sustain	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	4 vs Sustain	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C5	5 vs Sustain	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	6 vs Sustain	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C7	7 vs Sustain	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C8	3-1	-1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C9	5-1	-1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	6-1	-1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	7-1	-1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C12	7-6	0	0	0	0	0	0	0	0	0	0	-1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C13	3-6	0	0	0	0	1	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C14	5-6	0	0	0	0	0	0	0	0	1	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C15	3-7	0	0	0	0	1	0	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C16	5-7	0	0	0	0	0	0	0	0	1	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

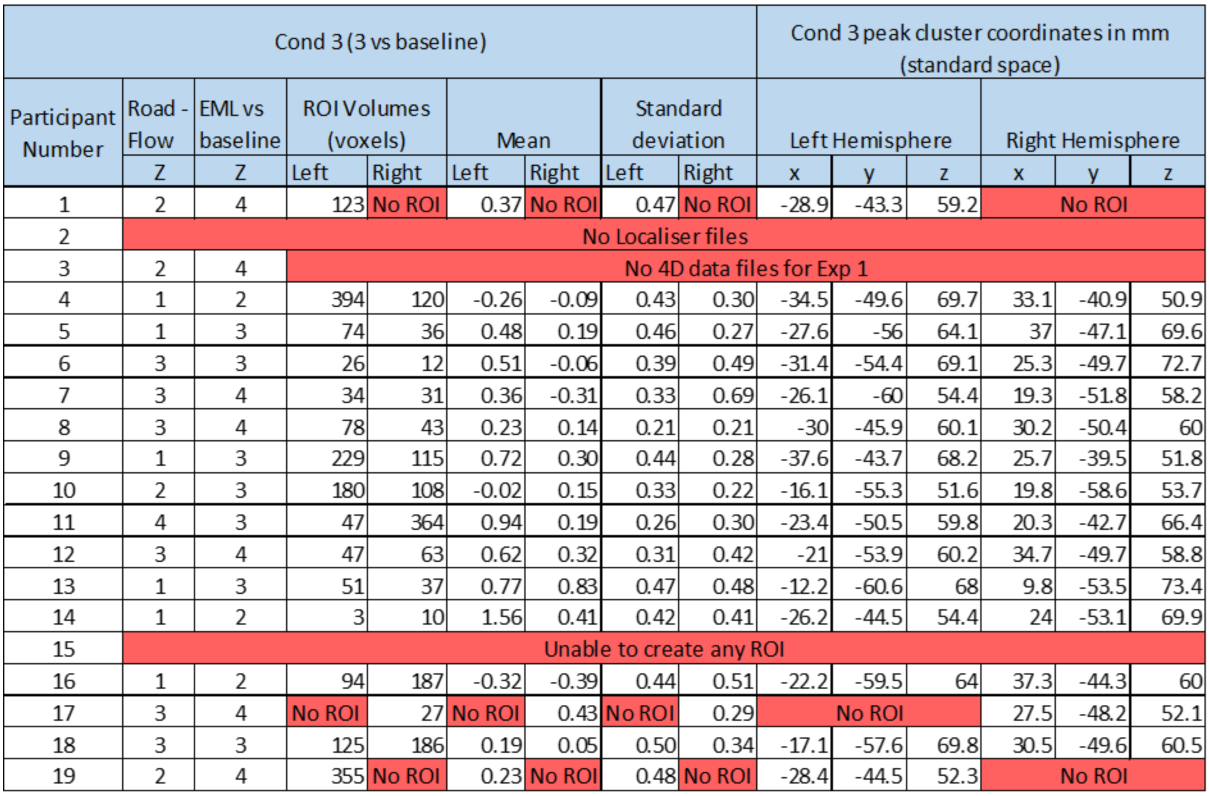
Figure 2.5.5. Design Matrix for the first experiment detailing the EVs for the 7 conditions versus sustain (baseline condition) and the contrasts that were performed. Temporal derivatives were added alongside a Volterra expansion of the estimated head motion parameters.

We used cluster thresholding throughout this thesis with an initial voxelwise threshold of z =3, and cluster *p* threshold of < 0.05 for all experiments conducted. This cluster threshold was used for all whole brain analysis initially at first level and then with higher level group analysis. At group level, each of the participants first level data was combined to provide the group analysis using FEAT (Woolrich, Ripley et al., 2001; Woolrich, Behrens et al., 2004). Each contrast produced a whole brain activation map at both first level and group level. To further determine whether the brain area we are interested in produced any activation in the contrast that were analysed, a region of interest (ROI) data analysis was completed.

2.5.8 ROI data analysis

The ROI masks were created using the localiser scans, specifically the *road* minus *flow* contrast and the *eye movement localiser* (EML) versus *baseline* contrast. Applying ApplyXFM (part of FLIRT Jenkinson et al., 2002; Jenkinson & Smith, 2001); to the results of each of the first-level localiser contrasts we were able to resample them to MNI standard space, then these contrasts could be displayed in FslView (part of the FRMIB software Library) on top of the participants own highRes2Standard image to allow for accurate location of observed activation. The initial voxelwise Z threshold, uncorrected for multiple comparisons, applied to these activation maps was 3. From this starting point, each of the two contrasts that were used to create the ROI mask had the voxelwise Z threshold adjusted individually. This was done to ensure that the ROI was as large as it could be without having excessive random activation around the regions of interest. (Genovese, Lazar, & Nichols, 2002; Valyear, Culham, Sharif, Westwood, & Goodale, 2006). ROI masks were drawn to include voxels that were active in the *road-flow* contrast that were also NOT active in the *EML* contrast (Billington et al., 2010; Field et al., 2007). The individual thresholds that were used to define the ROI masks, along with the ROI volumes and coordinates can be found in Table 2.5.6. As an additional constraint the Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) was used to highlight voxels that were categorized as being at least 20% likely to be in the SPL: only voxels falling within this area were included. ROI masks were created separately for the right and left hemispheres and were hand drawn slice by slice (see Figure 2.5.7. for an example).

Table 2.5.6. Individual z thresholds for each participant's data where a ROI mask was created. The masks used the *road – flow* contrast and the *EML* vs *baseline* contrast to identify the voxels that were activated in *road – flow* but were not activated in the *EML* vs *baseline* contrast. Volumes (voxels), mean of % signal change and standard deviations are also displayed for each ROI as well as the peak cluster coordinates in mm (standard space) for condition 3 vs sustain in both the left and right hemispheres.



Cond 3 (3 vs baseline)										Cond 3 peak cluster coordinates in mm (standard space)					
Participant Number	Road - Flow	EML vs baseline	ROI Volumes (voxels)		Mean		Standard deviation		Left Hemisphere			Right Hemisphere			
	Z	Z	Left	Right	Left	Right	Left	Right	x	y	z	x	y	z	
1	2	4	123	No ROI	0.37	No ROI	0.47	No ROI	-28.9	-43.3	59.2	No ROI			
2	No Localiser files														
3	2	4	No 4D data files for Exp 1												
4	1	2	394	120	-0.26	-0.09	0.43	0.30	-34.5	-49.6	69.7	33.1	-40.9	50.9	
5	1	3	74	36	0.48	0.19	0.46	0.27	-27.6	-56	64.1	37	-47.1	69.6	
6	3	3	26	12	0.51	-0.06	0.39	0.49	-31.4	-54.4	69.1	25.3	-49.7	72.7	
7	3	4	34	31	0.36	-0.31	0.33	0.69	-26.1	-60	54.4	19.3	-51.8	58.2	
8	3	4	78	43	0.23	0.14	0.21	0.21	-30	-45.9	60.1	30.2	-50.4	60	
9	1	3	229	115	0.72	0.30	0.44	0.28	-37.6	-43.7	68.2	25.7	-39.5	51.8	
10	2	3	180	108	-0.02	0.15	0.33	0.22	-16.1	-55.3	51.6	19.8	-58.6	53.7	
11	4	3	47	364	0.94	0.19	0.26	0.30	-23.4	-50.5	59.8	20.3	-42.7	66.4	
12	3	4	47	63	0.62	0.32	0.31	0.42	-21	-53.9	60.2	34.7	-49.7	58.8	
13	1	3	51	37	0.77	0.83	0.47	0.48	-12.2	-60.6	68	9.8	-53.5	73.4	
14	1	2	3	10	1.56	0.41	0.42	0.41	-26.2	-44.5	54.4	24	-53.1	69.9	
15	Unable to create any ROI														
16	1	2	94	187	-0.32	-0.39	0.44	0.51	-22.2	-59.5	64	37.3	-44.3	60	
17	3	4	No ROI	27	No ROI	0.43	No ROI	0.29	No ROI			27.5	-48.2	52.1	
18	3	3	125	186	0.19	0.05	0.50	0.34	-17.1	-57.6	69.8	30.5	-49.6	60.5	
19	2	4	355	No ROI	0.23	No ROI	0.48	No ROI	-28.4	-44.5	52.3	No ROI			

Once the ROI were created, Featquery, a program that is part of FEAT (Woolrich, Behrens et al., 2004; Woolrich, Ripley et al., 2001), was used with the ROI masks to retrieve mean stat values in each ROI for the percentage of BOLD signal change for each contrast used in the first level analysis. These were then analysed with ANOVA in SPSS.

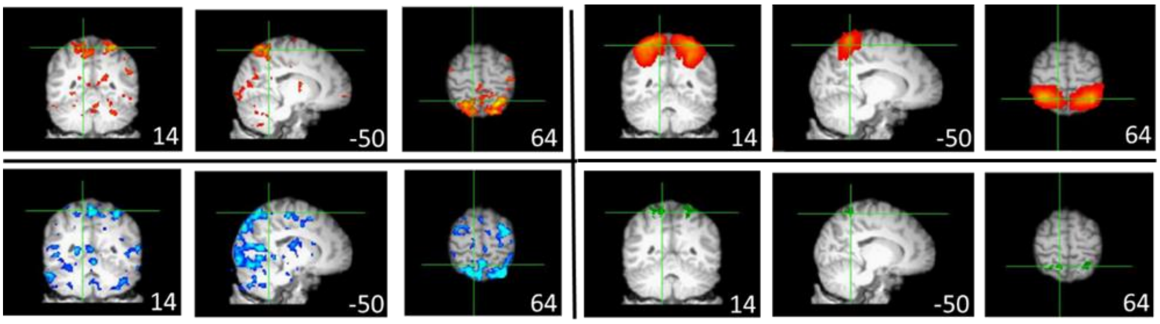


Figure 2.5.7. Example individual participant data highlighting the contrasts used to create the ROI mask. Top left panel: *road* minus *flow* contrast (threshold min 2, max 5). Bottom left panel: *EML* vs *baseline* contrast (threshold min 3, max 5). Top right panel: Unthresholded map of SPL atlas from Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006), although a threshold that gave a 20% probability that a voxel was in the SPL was used for ROI masks. Bottom right panel: ROI mask

2.6 Results

2.6.1 Behavioural Task

The behavioural task of this experiment was to determine that the participants were able to identify dimming events using a button press. During piloting, we verified that the code worked, and the response rate was calculated at 80-90% correct which provided reassurance that participants would be able to accurately identify the dimming event. However, when the behavioural task data was analysed for the remaining participants it became evident that there was a problem with the raw data files, they had recorded a large number of false trigger alarms. Due to the nature of the similarity and volume (400-500) of false alarms per participant it is more likely to be a malfunction of the equipment rather than human error. This has unfortunately resulted in unusable behavioural task data.

2.6.2 Shifting Spatial Attention hypothesis

Each of the seven experimental conditions was contrasted with the baseline at the individual participant level, and then a group average analysis was performed on these, where the baseline (condition 0) consisted of a single static square. To replicate the results of the Vandenberghe et al., (2001) study, activation was required in conditions 3 and 5. They consisted of a fixation cross, and a target square that would be viewed covertly or overtly (highlighted by the cueing circle). The target square moved horizontally to one of 10 pre-determined locations across the screen to drive the shifting of spatial attention that Vandenberghe et al., (2001) hypothesized as the function of the SPL. For conditions 3 and 5, activation was indeed detected in both conditions. (see Figure 2.6.1.). A whole brain conjunction analysis was applied to condition 3 vs sustain and condition 5 vs sustain separately to determine which voxels are present in both. Activation was observed in the left hemisphere (see Figure 2.6.2.). The coordinates x20, y-60, z60 and x-20, y-60, z60 are used throughout the thesis to indicate the SPL coordinates of interest and was produced by averaging the SPL peak coordinates from the eleven published papers reviewed in Chapter 1.

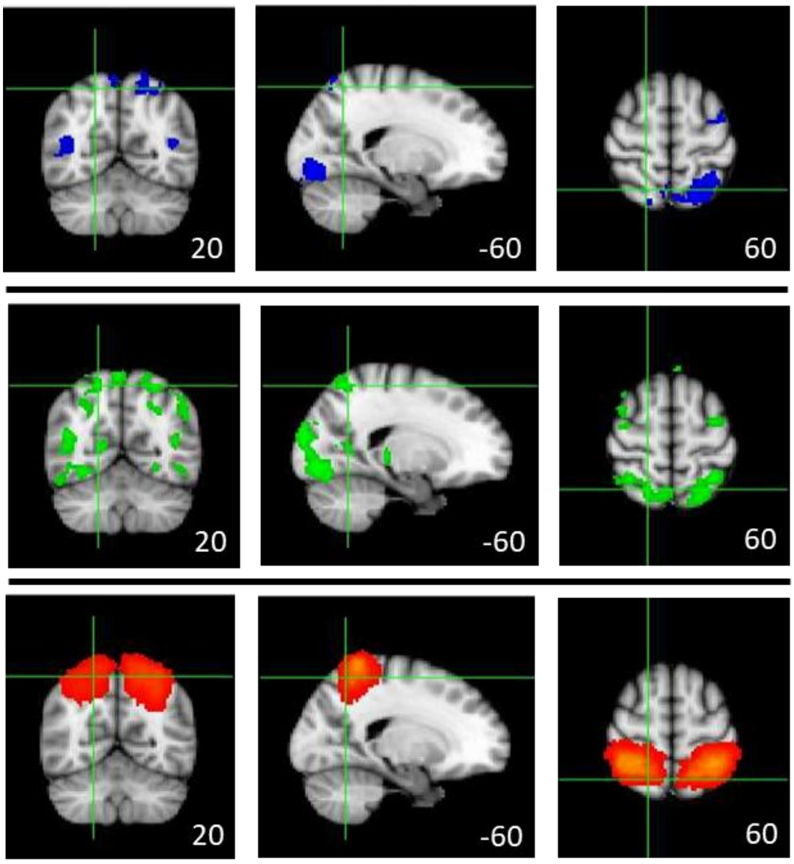


Figure 2.6.1. Top: condition 3 (covert shifting) minus sustain shows activation in the left hemisphere within the SPL; middle: condition 5 (overt shifting) shows bilateral activation within the SPL; bottom: Unthresholded map of SPL atlas from the Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006). Voxelwise threshold z= 3, with a cluster p threshold <0.05.

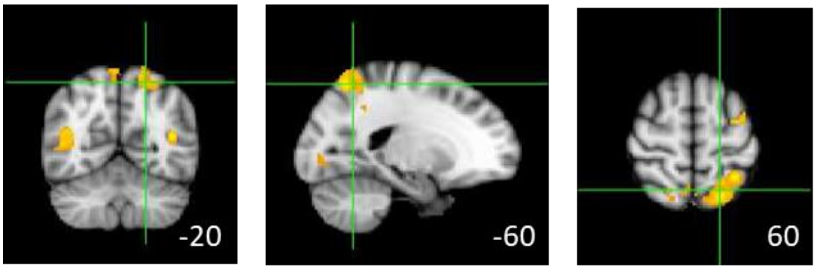


Figure 2.6.2. Whole brain conjunction analysis for conditions 3 vs sustain and 5 vs sustain (sustain condition consisted of a single static square). The overlapping voxels in conditions 3 and 5 had a voxelwise threshold of z=3, with a cluster p threshold <0.05.

2.6.3 Vandenburghe replication ROI analysis

The contrasts that were created to form the region of interest masks consisted of the *road* minus *flow* contrast and the *eye movement localiser* versus *baseline* contrast described in detail earlier. When the target stimulus displaces, a higher BOLD signal change is expected in the SPL under the attention shifting hypothesis compared to target stimuli that did not displace, but attention is maintained in the same way. Featquery was used to determine the percentage of signal change and it showed that conditions 3 and 5, in which stimulus displacement did occur, maintained a higher percent signal change when compared with the static conditions (condition 2 and 4) (see Figure 2.6.3.). The left hemisphere ROI produced a higher percentage of signal change in both the moving conditions (3 & 5) and static conditions (2 &4) compared to the right hemisphere ROI.

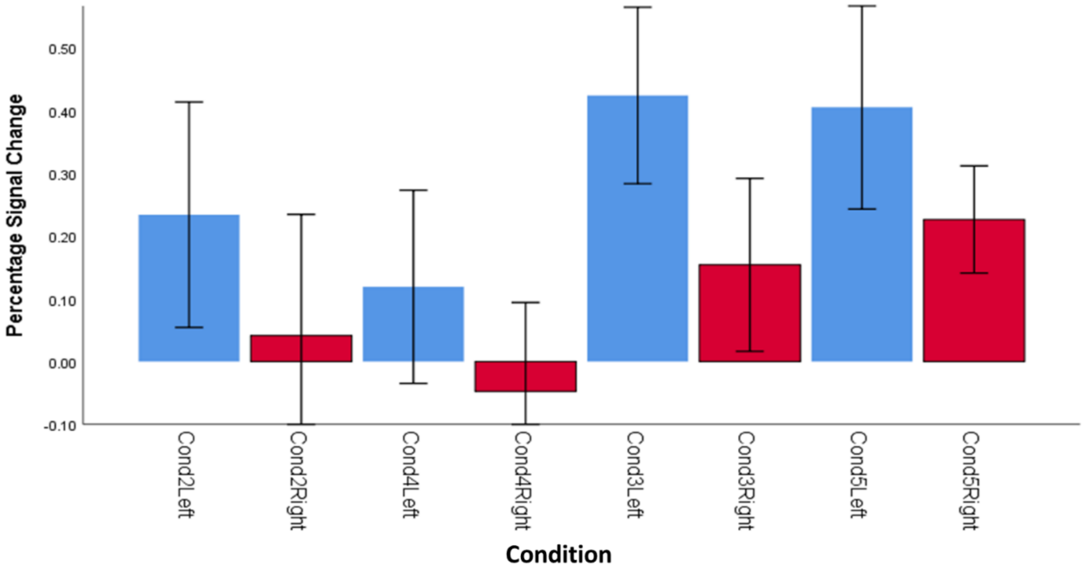


Figure 2.6.3. A higher percentage signal change is observed for the displacing conditions (3 and 5) compared to the static conditions (2 and 4). Missing data is mean substituted. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

A 2x2x2 (Hemisphere (left, right) x Attention type (covert – conditions 2 and 3, overt – condition 4 and 5) x Displacement (moving – conditions 3 and 5, static – conditions 2 and 4)) repeated measures ANOVA was conducted to further explore the results. Missing data was replaced with mean substitution. The main effect of hemisphere was just significant (*F* (1,15) = 4.780, *p*=.045, ηp^2 =.242). The main effect for attention type was not significant (*F* (1,15) = 0.563, *p*=.465, ηp^2 =.036). However, as predicted by the attention shifting hypothesis the main effect for displacement was significant (*F* (1, 15) = 15.837, *p*=.001, ηp^2 = .514). Each of the interactions were not significant with hemisphere and displacement (*F* (1,15) = .399, *p*=.537, ηp^2 = .026), attention and displacement (*F* (1,15) = 1.866, *p*=.192, ηp^2 = .111) and hemisphere and attention (*F* (1,15) = 0.462, *p*=.507, ηp^2 = .030). The interaction between hemisphere and attention type and displacement was also not significant (*F* (1,15) = .231, *p*=.638, ηp^2 = .015.

These results need to be further explored under the visual separation hypothesis specifically looking at condition 1 which consists of the single square displacing.

2.6.4 Visual Separation Hypothesis

The experimental conditions that were replications of Vandenberghe et al., (2001) produced similar results to the original paper, and therefore are consistent with the attention shifting hypothesis. Condition 1 was added to further test the attention shifting hypothesis because under this hypothesis activation would be predicted since the target square displaced to different locations. Condition 1 consisted of a single square that displaced horizontally which was tracked by overt eye movements.

Importantly, no activation at coordinates was observed for this stimulus contrasted with sustaining baseline at a cluster threshold z=3, which was the threshold used throughout the whole thesis. There is, however, activation produced at a more liberal cluster threshold z=2.3. (see Figure 2.6.4.).

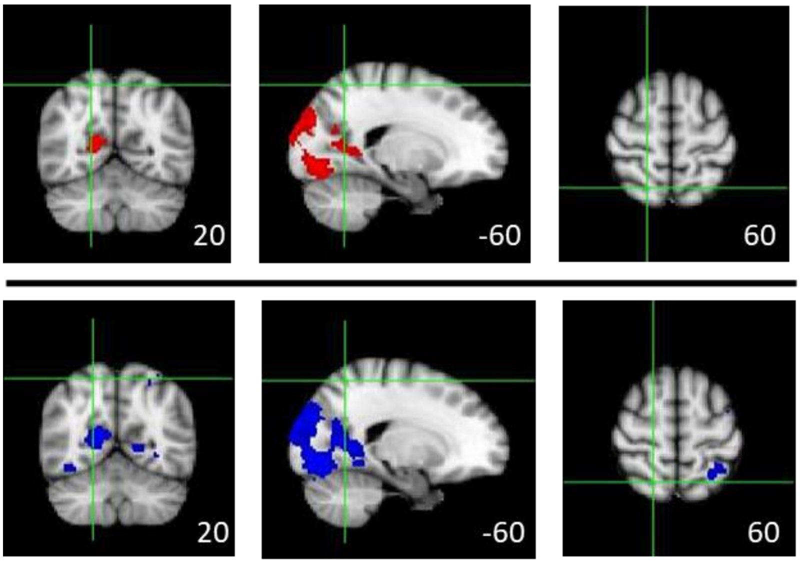


Figure 2.6.4. Top: condition 1 (single square displacing) produced no activation at coordinates in the area of interest compared to the sustaining attention baseline at cluster threshold z=3, with a cluster p threshold <0.05. Bottom: condition 1 produced an area of activation in the SPL when a more liberal voxelwise threshold z=2.3 was applied, with a cluster p threshold <0.05.

The whole brain analysis results for condition 1 refutes Vandenberghe et al., (2001) shifting spatial attention hypothesis when using the standard cluster threshold. Examining the difference in signal change across the displacing conditions will provide more information regarding the key condition 1. Turning to the ROI analysis, Figure 2.6.5. presents the key comparison between conditions 1, 3 and 5.

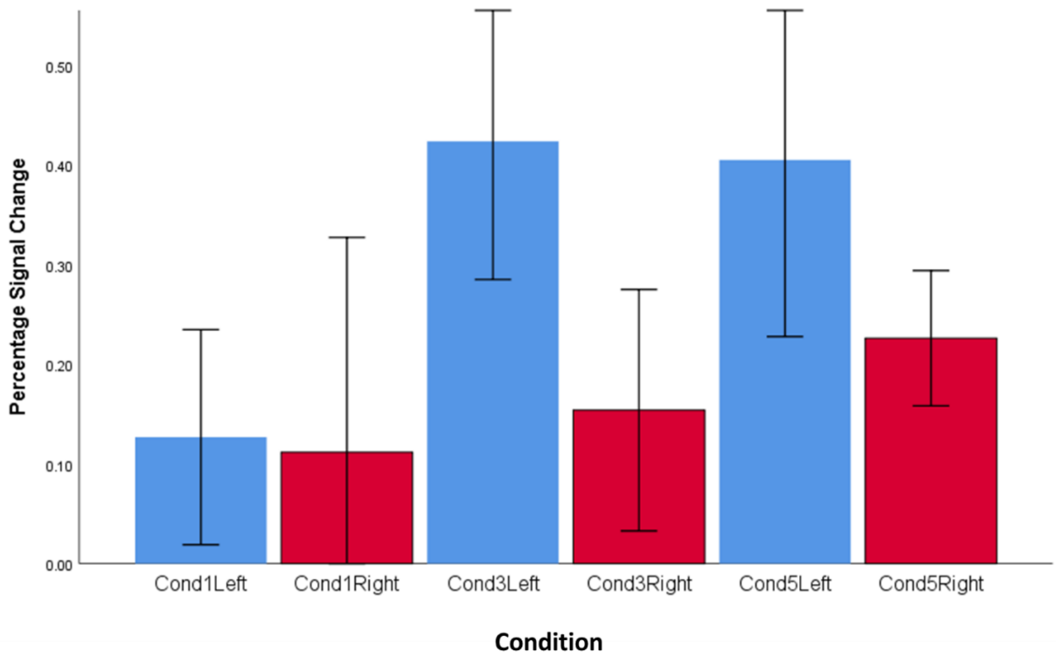


Figure 2.6.5. ROI percentage signal change of displacing conditions 1, 3 and 5. Conditions 3 and 5 represented overt and covert viewing conditions of the target square and included a fixation cross whereas condition 1 was a single displacing target square. Missing data is mean substituted. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

A 2 (Hemisphere: left, right) x 3 (condition: 1,3 and 5) repeated measures ANOVA was performed to specifically look at the displacing conditions in more detail. Missing data was mean substituted, and sphericity was assumed. The main effect for hemisphere was not significant (F (1,15) = 2.712, p = .120, ηp^2 = .153), whereas the main effect for condition was significant (F (2,30) = 4.091, p =.027, ηp^2 = .214) and the interaction between hemisphere and condition was also significant (F (2, 30) = 4.285, p =.023, ηp^2 = .222). Reviewing Figure 2.6.5. indicates that the main effect for condition was driven by the difference between condition 1 and the other two conditions (3 and 5). This was confirmed with a 2 x 3 special contrast ANOVA (IBM SPSS Statistics 25

Command Syntax Reference) with a fully repeated design and the main effect was significant (*F* (1,15) = 6.191, *p* = 0.25). The significant interaction showed a larger difference between condition 1 and the other two conditions in the left hemisphere of the brain than the right.

As an additional test, a one sample t-test was performed on condition 1 to see if the signal change generated was significantly higher than the static sustaining baseline. Prior to performing this t-test the data was collapsed across the two hemispheres. The t-test was not significant *t* (15) = 1.73, p = .104 which shows that the signal in condition 1 is not significantly different from the sustaining baseline. This therefore refutes the shifting spatial attention hypothesis and is consistent with the visual separation hypothesis.

2.6.5 Divided Attention hypothesis

Conditions 3 and 5 consisted of either covert or overt attention to the target square and activated the region of interest while condition 1, which consisted of overt attention to a single moving square, did not activate the SPL region of interest. The divided attention hypothesis states this difference is due to the absence of divided spatial attention from condition 1 that was potentially present in conditions 3 and 5. As conditions 1, 3 and 5 are unable to fully answer this, additional conditions are required for further exploration. The added experimental conditions will specifically examine the divided attention hypothesis and subsequent predictions. Conditions 6 and 7 were created to further divide the participants attention with condition 7 providing visual stimuli that required the viewer to attend to two locations (both the upper and lower squares) whereas in condition 6 the viewer is only needed to attend to one location (the upper square). The viewer fixated on the fixation cross throughout these two conditions. Under the divided attention hypothesis, condition 7 predicted higher activation compared to the less divided condition 6. This prediction was not supported by the whole brain contrast analysis of 7-6 at cluster threshold of z = 3 or at the reduced cluster threshold of z = 2.3. This contrast shows that there was not any significant difference between the two conditions, this therefore refutes the divided attention hypothesis (see Figure 2.6.6., bottom left and bottom right panels).

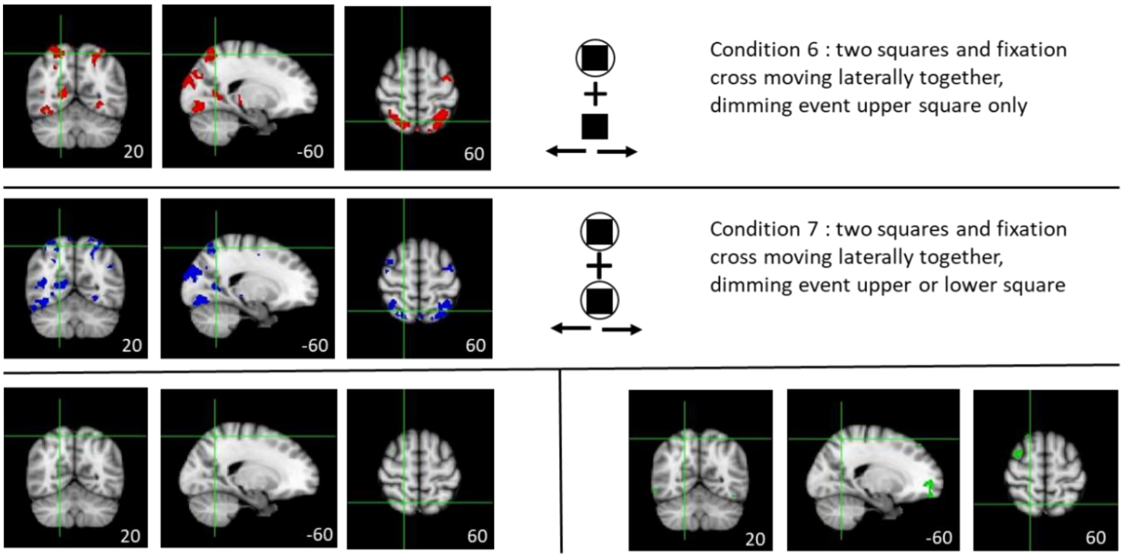


Figure 2.6.6. Top: condition 6 at cluster threshold z=3, with a cluster p threshold <0.05 and visual stimuli for that condition where the arrows depict lateral displacement to one of the 10 pre-determined locations; middle: condition 7 at cluster threshold z=3, with a cluster p threshold <0.05 and visual stimuli, arrows depict displacement as the condition 6; bottom left: contrast condition 7 minus condition 6 at cluster threshold z=3, with a cluster p threshold <0.05; bottom right: same contrast at same coordinates but with a more liberal cluster threshold of z=2.3, with a cluster p threshold <0.05.

To further test for differences in SPL activation due to the division of attention, a ROI analysis was performed. Figure 2.6.7. presents the signal change for conditions 6 and 7 in the left and right hemisphere ROI. A 2 (Hemisphere: left, right) x 2 (Divided Attention: Encouraged in condition 7, not encouraged in condition 6) repeated measures ANOVA was performed. Missing data was mean substituted, and sphericity was assumed. The main effects for hemisphere (*F* (1, 15) = 2.489, *p* = .136, ηp^2 = .142) and divided attention (*F* (1,15) = .242, *p* =.630, ηp^2 = .016) were not significant. The interaction between hemisphere and divided attention was also not significant (*F* (1, 15) = .278, *p* = .606, ηp^2 = .018). These results fail to support the divided attention hypothesis for the function of the SPL. The difference observed between conditions 1 compared to 3 and 5 is therefore unlikely to be due to the processes of dividing attention being involved.

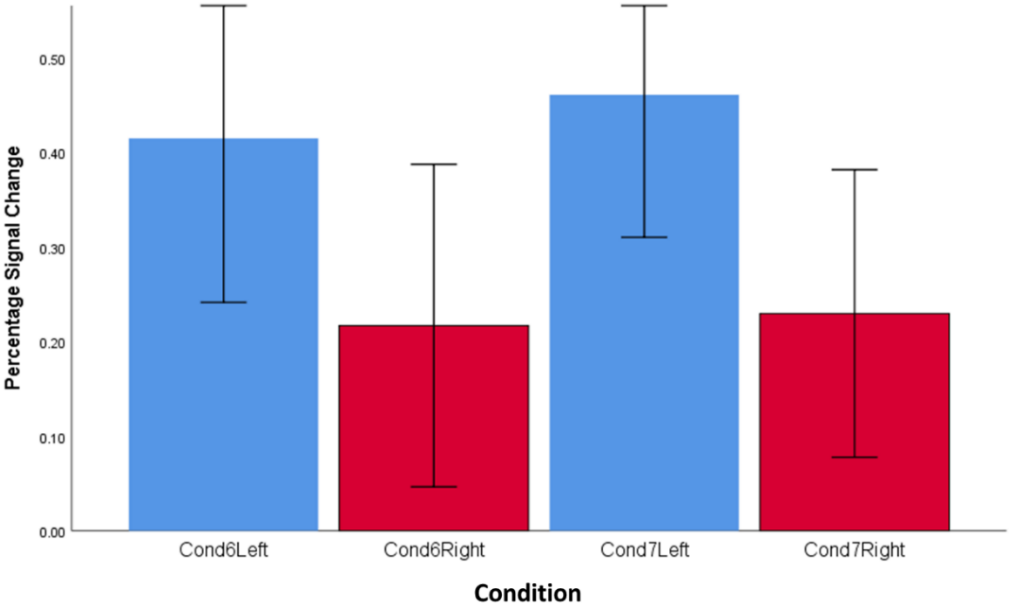


Figure 2.6.7. Percentage signal change of the ROI between conditions 6 and 7 in the left and right hemisphere. Missing data is mean substituted. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

2.6.6 Visual Separation hypothesis- further explored

It has already been noted that condition 1 did not significantly activate the SPL at cluster threshold z=3 and had a low BOLD response at a more liberal threshold that did not produce significant ROI analysis results, and this thereby increases the likelihood that visual separation hypothesis is the more plausible function of the SPL. However, for conditions 6 and 7, the visual separation hypothesis expects to perform as condition 1 which consists of a solitary element and has no visual separations. This is because the multiple elements that make up the visual stimuli for these two conditions, whilst there are visual separations between them, these remain constant and therefore any initial neural response to them at the start of each block in the block design should have rapidly adapted as is typically found in fMRI (Grill-Spector & Malach, 2001; Malach, 2012). Whereas conditions 3 and 5, with the adding of a fixation cross that remains static throughout the task, clearly has a new visual separation between the target square and the fixation cross every time the target square displaces to a new location. This prediction was not supported by the data, Figures 2.6.6. and 2.6.7. shows strong activation in SPL versus the sustained baseline for both conditions 6 and 7.

Figure 2.6.8. presents signal change in the SPL ROI, comparing conditions 6, 7 and 1. A 2 (hemisphere: left, right) x 3 (condition: 6, 7, and 1) repeated measures ANOVA was performed. Missing data was mean substituted, and sphericity was assumed. The main effect for hemisphere and the interaction between hemisphere and condition was not significant (F (1,15) = 1.493, p = .241, ηp^2 = .091) and (F (2, 30) = 2.477, p = .101, ηp^2 = .142) respectively. However, the main effect for condition was significant (F (2, 30) = 4.562, p = .019, ηp^2 = .233). Figure 2.6.8. shows that especially

for the left hemisphere conditions 6 and 7 differ significantly from condition 1. However, when the special contrast fully repeated ANOVA was performed the main effect for condition was not significant (*F* (1, 15) = 1.827, *p*=.197) which could be due to the less obvious differences between the right hemispheres across conditions.

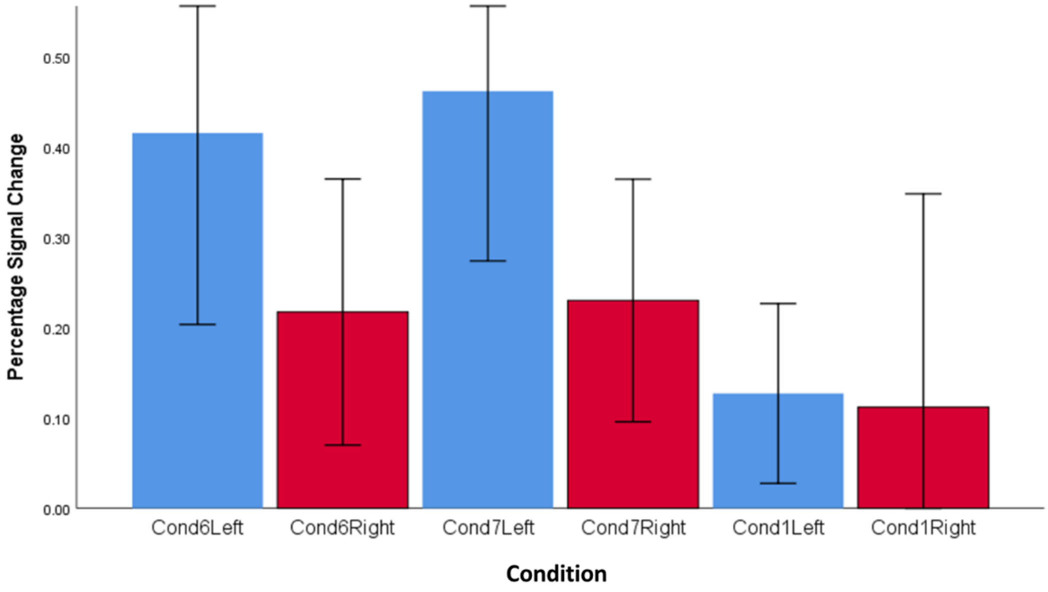


Figure 2.6.8. Percentage signal change of ROI for conditions 6, 7 and 1 in the left and right hemispheres. Missing data is mean substituted. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

2.7 Discussion

This experiment produced interesting results, some of which were predicted and some of which were unexpected. The activation observed within the SPL (at and near coordinates x20, y-60, z 60 and x-20, y-60, z60) for the conditions that contained a static fixation cross and a displacing square, whether viewed covertly or overtly by the participant (conditions 3 and 5), were predicted by both the visual separation and attention shifting hypotheses. It was also found as expected that for the conditions where the objects remained static (the fixation cross and the target square) that there would be no or minimal activation relative to the sustaining baseline observed at or near the coordinates of interest. The visual separation hypothesis correctly predicted that for the key condition (condition 1) there would be no significant activation in the SPL for a single square displacing laterally without a fixation cross, while the spatial attention shifting hypothesis incorrectly predicted that activation would be found in this condition. The divided attention hypothesis predicted that condition 7 would have greater activation in the SPL than condition 6 due to attention being divided across two elements compared to one element in condition 6. This however did not occur. The visual separation hypothesis predicted a low BOLD response to both 6 and 7 because the visual separation between the elements remained constant, however the opposite occurred, and a high BOLD response was observed in both conditions. These results do not strongly support any of these initial hypotheses.

The key condition for the visual separation hypothesis was condition 1 which consisted of a single displacing square. Under this hypothesis activation was not expected because there was only one object being observed by the participant and therefore nothing for visual separation to be calculated against. Visual separation needs two or more objects for it to be perceived and it is not possible with a solitary object. The lack of activation for this condition is consistent with the visual separation hypothesis. It therefore also refutes the shifting spatial attention hypothesis as investigated in the Vandenberghe et al., (2001) study because the displacement parameters were kept consistent with the other displacing conditions (conditions 3 and 5). Therefore, if activation in the SPL was just caused by tracking displacements with shifts of spatial attention it would also have been expected in the SPL area for condition 1.

The significance of the fixation cross has been emphasised at the beginning of this chapter and has been a prominent feature in many visual attention studies as a way of allowing the participant to fixate at a central point and attend to peripheral locations. Fixation crosses are commonplace in psychological experiments to maintain a participant’s gaze to a specific location. These fixation crosses allow consistency between trials and participants for parameters such as eye tracking or attention where it is necessary for it to be controlled or for saccades to be minimised. The fixation cross is seen as separate to any other visual stimuli and as a necessity to allow comparison across participants. They can also be used to covertly view other visual stimuli such as in Vandenberghe et al., (2001) study and the first experiment of this thesis. However, as we have shown the seemingly task-irrelevant fixation cross fundamentally changes the participants experience of many typical visual stimuli, thus showing that the fixation cross has become task relevant. Our results suggest that planning of future studies should consider the impact a fixation cross may have on the experimental results.

The high level of activation in conditions 6 and 7 was unexpected. The individual target squares making up the stimuli in these two conditions displaced together and we therefore assumed that they would be perceived as one object. Such as with the Gestalt principle of proximity where elements within a scene that are within a close proximity to each other are therefore grouped together (Bruce, Green & Georgeson, 2003). Visual separations between the different elements of the visual stimuli in these two conditions were present but as they remained constant when they displaced, activation was not expected due to neural adaptation. Whilst we predicted no significant activation, the opposite occurred with high activation observed in both, so could multiple elements used to make the stimuli be directly responsible for the high activation? The answer is no, because in conditions 2 and 4 which also consisted of multiple elements (fixation cross, target square and cueing circle) but were static and therefore the visual separations remained constant and low BOLD activation was observed in the SPL, consistent with neural adaptation. Whereas the shifting attention hypothesis did predict activation in condition 1 and that did not occur. This therefore makes it unlikely that the shifting spatial attention hypothesis is correct. A possible explanation as to why conditions 6 and 7 activated SPL but conditions 2 and 4 had low activation will be explored below.

The shifting spatial attention hypothesis can explain the results of conditions 3 and 5 but it does not explain the lack of BOLD signal in the SPL for condition 1. Each of these conditions involved the visual stimuli to displace which caused a shift in spatial attention so then why did condition 1 not activate the SPL like conditions 3 and 5 did? Likewise, we observed high activation in conditions 6 and 7, where the participants were required to divide their attention between two elements in condition 7 and one element in condition 6. Conditions 2 and 4 also contained multiple elements, where condition 2 required the participant to covertly attend to the target square by fixating on a fixation cross in the same way as condition 6 does, but low activation was observed for this condition and condition 4 where the target square was viewed overtly. The results do not support the divided attention hypothesis.

These results provide a confusing answer to our research question concerning the function of SPL as each hypothesis had both supporting and refuting results. A better understanding of why we got the results is needed. After much deliberation, we believe that the nature of how the target square(s) arrived at their pre-determined locations could hold the key to explaining the results observed in this experiment. When observing the visual stimuli given to participants it became evident that target displacements made it appear as if the target stimuli had ‘jumped’ to its new location. The target squares next location could be closer or further away from its current location, especially because of the parameters that were used to replicate Vandenberghe et al., (2001) study which meant that the displacements could be quite large and provided more chances of ‘jumping’ right across the screen to locations not directly next (to the left or right) of the previous location.

Our next experiment was devised to explore this proposal and determine if the ‘jumping’ effect impacted on the activation in the SPL. We believe that the ‘jumping’ of the visual stimuli could be breaking neural adaptation, so that neurons tuned to a particular value of visual separation would treat each new appearance of the stimuli as novel and re-calculate the visual separation between the multiple elements (if present). This re-calculation would happen in conditions 6 and 7, but not 1, due to the absence of visual separations from the stimuli. The results for conditions 2 and 4 which had low BOLD response are consistent with this proposal and the possibility of removing the ‘jumping’ effect, but still displacing visual stimuli could provide more answers. The next experiment will investigate this proposal.

Chapter 3 – Experiment 2

3.1 Review of experiment 1

Experiment 1 produced expected results for conditions 3 and 5 that followed the constraints of the Vandenberghe et al., (2001) study. Experiment 1 replicated Vandenberghe’s results where activation was observed in overt and covert viewing conditions of a target square displacing laterally. However, to explore the shifting spatial attention hypothesis and visual separation hypothesis further, condition 1 was added. This condition consisted of a single target square displacing and with the absence of the fixation cross that was present in conditions 3 and 5, the visual separation hypothesis would expect no significant activation. This would be due to the lack of visual separation when only one object is present compared to conditions 3 and 5 that contained a fixation cross for each condition. Whereas the shifting spatial attention hypothesis would still expect to see activation. No significant activation was observed in the SPL, at cluster threshold 3, refuting Vandenberghe et al.'s, (2001) shifting spatial attention hypothesis and this result showed support for our visual separation hypothesis.

The results for the static conditions 2 and 4 also provided support for the visual separation hypothesis because whilst there were multiple objects present: target square, cueing circle and fixation cross, the lack of displacement meant that the visual separation between the objects was fixed, there were no changes of lateral displacement to create changes in visual separation.

In addition to these hypotheses, we also examined whether the division of attention between multiple objects could explain activation in the SPL. Using the target squares that were positioned at the top and bottom of the fixation cross, there was a single cueing circle on the upper square for condition 6 and two cueing circles (upper and lower) for condition 7. Participants' attention was divided between the upper and lower squares in condition 7, where fixation on the fixation cross meant they had to covertly attend to two locations to identify the dimming event. To restrict visual separation the objects in the visual stimuli displaced in unison. This eliminated the visual separation changes because visual separation remained constant throughout the trial, therefore the conditions would be investigating elements of divided attention only (see Figure 3.1.1). This meant that the visual separation did not change throughout the trials. The results from these two conditions were unexpected; the lack of difference between the two conditions did not support the divided attention hypothesis, and because the activation was high in both conditions, the visual separation hypothesis was also not supported because it predicted low activation in both conditions. What could explain the activation in the SPL that was being observed? We believe that the answer to that is how the objects displaced across the screen. After examining the visual stimuli and watching how it was presented to the participants, it became apparent that the movement of the objects appeared to 'jump' or 'teleport' to the next location. This was even more apparent when the objects moved a distance away from the previous location. We began to wonder if this 'teleportation' could be playing a part when multiple objects were present? In condition 1 a single object did not activate SPL when it 'teleported' to its new locations, but it did activate the SPL brain region when there were multiple objects. Could the 'teleportation' effect be part of a dual process explanation where basic neural adaptation could also play a part when looking primarily at the way the objects moved to the different locations? This was an element that we did not consider when designing experiment 1.

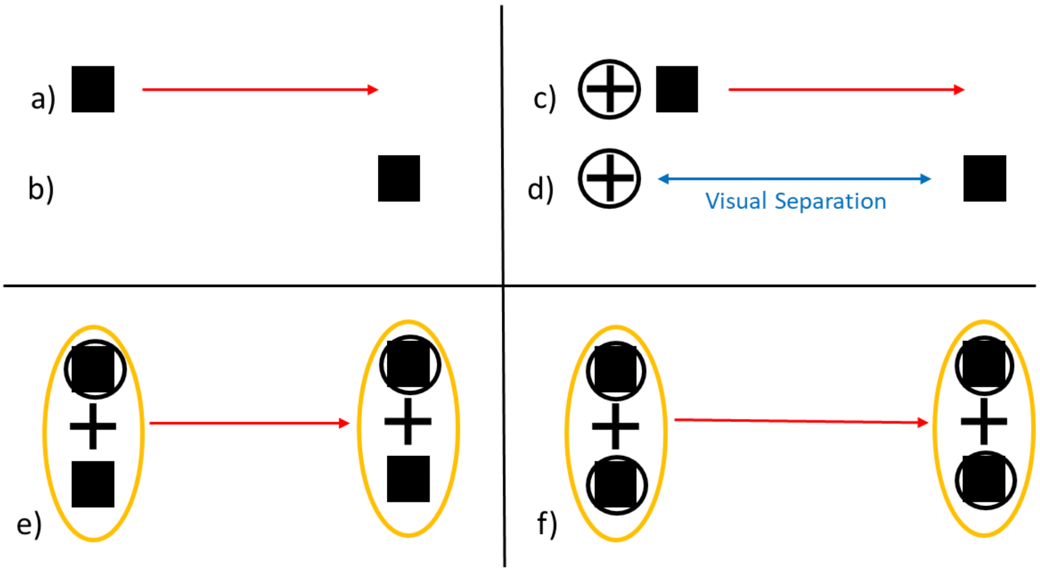


Figure 3.1.1. Top left panel: a) condition 1 consisting of a single square displacing (red arrow depicts lateral movement); b) shows new location of the single square. Top right panel: c) condition 3, covert viewing of target square (red arrow depicts lateral movement); d) shows new location of the target square leaving the fixation cross and cueing circle in its original place (blue line shows the change in visual separation that has occurred between the static objects and the new location of the target square after displacement. Bottom left panel: e) condition 6 where all the objects (two squares, cueing circle, and fixation cross) move in unison (orange oval depicts the movement together). Bottom right panel: f) condition 7 where all objects (two squares, two cueing circles, and fixation cross) move in unison (orange oval) to the new location therefore no visual separation occurs. Again, for these two panels the red arrow depicts lateral movement.

3.2 Adaptation

Adaptation is well known within vision perception, indeed without adaptation our perception of the world would be very different. Behavioural adaptation allows the brain to ignore certain elements once they are deemed unimportant and is vital to allow us to maintain concentration on elements that are of importance either for a current task or something that needs attending too e.g., to establish if something is a threat or not. With the advent of neuroimaging, adaptation has been used with fMRI to determine which neural populations are involved in adaptation, a technique known as functional magnetic resonance adaptation (fMR-A) (Grill-Spector, Kushnir, Edelman, Avidan, Itzchak, & Malach, 1999). fMR-A can demonstrate that when a stimulus is repeated, the BOLD signal it produces reduces over time, as the neurons that are invariant to those stimulus properties adapt to their repeated presence. If the stimulus is then manipulated in some way and the BOLD signal increases the neurons that are tuned to that manipulation produce the increase in BOLD signal (Grill-Spector & Malach, 2001; Malach, 2012).

Prior to fMR-A, single cell studies were mainly utilised to observe adaptation at a neuronal level. Animal studies provided insight into adaptation of factors such as visual orientation in the striate cortex of the macaque (Muller, Metha, Krauskopf, & Lennie, 1999) and movement direction in the medial temporal area of the rhesus monkey (van Wezel & Britten, 2002) however, due to their invasive nature single cell procedures are not viable for the majority of human studies and an alternative non-invasive way of observing adaptation was found with neuroimaging techniques. fMR-A was able to provide this non-invasive way to measure the BOLD signal to determine adaptation for a variety of parameters, examples include orientation (Fang, Murray, Kersten, & He, 2005); motion (Konen & Kastner, 2008) and faces (Xu, Yue, Lescroart, Biederman & Kim, 2009), for a review of fMR-A in these three areas see Krekelberg, Boynton, & van Wezel, (2006).

Within the posterior parietal cortex region, fMR-A has been used to investigate processing of eye movements and motion. In a study by Konen & Kastner, (2008) they tested adaptation to motion in three types of visual stimuli representing optic flow (planar, circular, and radial). The stimuli consisted of random dots and for the adaptation tasks they displaced in one direction and for the non-adapted tasks they would displace in different directions. Their results showed adaptation effects were present in their region of interests they were investigating including the SPL (x17, y-73, z51 MNI[7]). The SPL did not show any greater adaptation to any of the three optic flow types, compared to the IPS region that found there was greater adaptation for radial flow.

The effects that were found in this study show that adaptation can occur when visual stimuli displace and studies such as these provide evidence of specifically tuned neurons that, after a length of time, reduced neural activity to that particular stimulus property and continued to do so unless that stimulus property changed in a particular way. This would then effectively break adaptation as new neurons that were sensitive to that change would increase the BOLD signal. In experiment 1, we believe that the way the target squares displaced was breaking adaptation and by manipulating the

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[7] To keep all coordinates within the thesis as MNI coordinates, those studies that reported talaraich coordinates were converted to MNI coordinates. We used MNI<->TAL (Yale University BioImage Suite Web 1.0.0., 2018 to achieve this.

way the target squares moves here will help contribute to determining which neurons are sensitive to visual separation changes within the SPL.

3.3 Teleportation

The shifting element of the visual stimuli in conditions 6 and 7 as well as conditions 1,3 and 5 were bound by the constraints of the Vandenberghe et al., (2001) study, due to the replication we were trying to achieve. Therefore, the target square(s) would displace to one of the 10 pre-determined locations described in chapter 2 (see Figure 3.3.1). The shifts of the visual stimuli consisted of a third displacing to the left-hand side, a third to the right-hand side and a third across the midline. They were in a pseudo randomised order created using the random function in our Matlab code. The only time the target square(s) stayed in the same location for an iteration was during a null event, which occurred at random times throughout a trial unique for each participant. These constraints meant that the target square would make often quite large 'jumps' across the screen making the stimuli appear to 'jump' or 'teleport' to a new location. For conditions 6 and 7, participants are asked to fixate on the fixation cross, attend to one or two target squares and make saccades to each new location that the visual stimuli displaced to, but the constraints remained the same. The only difference being that all the elements of the visual stimuli moved in unison.

Adaptation suggests that a repeated stimulus over time reduces the strength of the BOLD signal, however, could the shifting movement itself be 'breaking' adaptation resulting in the proposed visual separation tuned neurons to recalculate the visual separation between the multiple elements of the triplet stimulus each time it displaced to a new location? The displacement of the target stimulus could trigger re-calculation of visual separation from the proposed visual separation tuned neurons whenever it ‘jumped’ or ‘teleported’ to its next location. Each ‘jump/teleport’ breaks adaptation that would be expected following the Gestalt proximity principle of treating all objects that are close to each other as one (Bruce et al., 2003), but instead the jump results in treating the elements as novel and re-calculating the different elements of the visual stimulus.

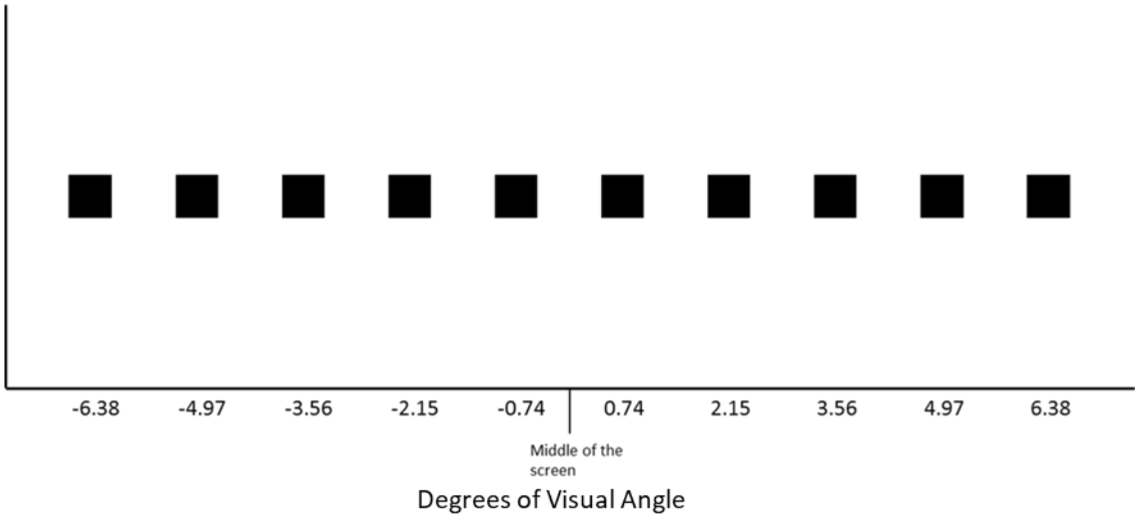


Figure 3.3.1: The ten pre-determined locations across the midline of the screen which was used within experiment 1 from the Vandenberghe et al., (2001) study (0.74, 2.15, 3.56, 4.97 and 6.38° on either side of the centre)

This proposed idea can be further explained by conditions 2 and 4 of Experiment 1 where, despite consisting of multiple elements (target square, fixation cross and cueing circle), but because of including no changes to visual separation (static stimuli), no significant activation was observed in the SPL region. This contrasted with the conditions where displacement occurred, and multiple elements were present (conditions 3, 5, 6 & 7) which all produced activation in the SPL. The only displacing condition where activation in the SPL did not occur was in condition 1, where the solitary target square had no other reference objects present to re-calculate visual separation to. Multiple objects are needed to create visual separation relative to each other, therefore, no re-calculation could take place because the proposed visual separation neurons would not be engaged, therefore adaptation was not broken for this condition.

The ‘teleportation’ of the visual stimuli warrants further exploration. If teleportation of the visual stimuli is ‘breaking’ adaptation, then creating similar stimuli that reintroduces adaptation would be consistent with the proposal that there are visual separation tuned neurons within the SPL ROI and make sense of the apparent contradictions in the results of Experiment 1. As we suspect that the teleportation displacement is causing the break in adaptation it would be pertinent to create visual stimuli that eliminate the teleportation aspect of displacement. If we removed the need for the proposed visual separation tuned neurons to need to perform re-calculations during the movement the visual stimuli had to make then due to the lack of change in visual separation, adaptation for these neurons would then be expected, despite a movement of the stimulus. This can be done by replacing ‘teleportation’ of the triplet stimuli with smooth translation.

3.4 Types of eye movements involved in tracking smoothly translating compared to teleporting stimuli

When tracking a visual target, it is necessary for the eye to keep the target on the fovea and smooth pursuit eye movements enables this to happen (van Donkelaar, Miall, & Stein, 2000). Smooth pursuit displacement keeps the tracking continuous and on a smooth trajectory. If the target suddenly appeared then a reactive saccade would be made because the visual target would be unforeseen (Zimmermann & Lappe, 2009). A visual stimulus that ‘jumps’ or ‘teleports’ to a new location, as in Experiment 1, which could be in one of ten different locations, reactive saccades will be made because the participant would not be able to predict where the target square would appear next. Whereas for a smoothly translating target, scanning saccades, which involve the participant to continuously track and fixate on a target where the target moved in a more predictable manner. Changing between translating and teleporting conditions will potentially change the corresponding saccade from scanning to reactive, respectively. To limit the effects of the differing saccades we have used an eye movement localiser within our region of interest masks to eliminate voxels that specifically activated due to eye movements and only included those remaining voxels that activated the SPL from a known SPL localiser contrast (*road – flow*).

Kimmig, Ohlendorf, Speck, Sprenger, Rutschmann, Haller et al, (2008) investigated the effects of smooth pursuit eye movements on visual and oculomotor systems in the brain relating to transformations of retinal, head-centred and space coordinates. Kimmig et al., (2008) used four conditions where the visual stimuli consisted of two dots separated from each other vertically. In the visual condition the upper dot was static and fixated by the participant and the lower dot displaced laterally; the oculomotor condition saw the two dots displaced together laterally and the upper dot was tracked by the participant’s eye movements; the visuo-oculomotor condition had the upper dot displacing and tracked by the eye and the lower dot was static, in the rest condition both dots remained static. Kimmig et al., (2008) results however showed that they found activation in the SPL on the right-hand side for the visual condition versus rest (x 26, y -54, z 66), and activation bilaterally in the oculomotor versus rest (x 28, y -52, z 64 and x -20, y -66, z 62) and visuo-oculomotor versus rest (x 28, y -52, z 62 and x -16, y -72, z 54) conditions. They found higher activation in the oculomotor and visuo-oculomotor conditions compared to the visual condition. It must be acknowledged that the oculomotor condition produced findings where activation was observed in the SPL, yet this visual stimulus comprised of two objects displacing in unison and visual separation did not vary; this finding is not consistent with the visual separation hypothesis, although it would have predicted the other results of the study.

Ohlendorf et al., (2010) study, which was discussed in chapter 1, used an extension of the paradigm used in Kimmig et al., (2008), where their conditions included a variation in the number of background dots (1, 4, 16, & 36). Unlike Kimmig et al., (2008) they reported that no PPC activation was observed for the oculomotor condition. Ohlendorf et al., (2010) observed greater activation in PPC including the SPL for the conditions that had the visual stimuli elements (target dot and background dots) displacing in opposite directions. They acknowledged that Kimmig et al., (2008) had PPC activation in the oculomotor condition when there was one background dot and one target dot, however, neither did Ohlendorf et al., (2010) get activation when they varied the number of background dots in their oculomotor condition. They attempted to explain the lack of activation to be related to the background dots being the frame of reference in relation to the target dot and the corresponding displacement between them.

Whilst this explanation from Ohlendorf et al., (2010) implies that differing motion between the background dots and target dots is relevant to the function of the

PPC and is supportive of the visual separation hypothesis, as noted above Kimmig et al., (2008) had differing results with similar stimuli. Therefore, our study can also be seen as resolving the contradiction between Kimmig et al., (2008) and Ohlendorf et al., (2010).

3.5 Hypotheses and predictions

This experiment is designed to clarify the results of experiment 1 with the intention of providing clearer statements regarding the visual separation and shifting spatial attention hypotheses. Stripping back some of the previous constraints of experiment 1 that replicated and expanded Vandenberghe et al., (2001) paradigm, this experiment will concentrate on the displacing of the target square(s).

As already discussed, the ‘jumping’ or ‘teleporting’ nature of the visual stimuli in the expanded portion of the Vandenberghe et al., (2001) study, conditions 6 and 7, potentially break adaptation with each ‘jump’ or ‘teleportation’ to its new location. Adaptation is predicted to be reintroduced when that ‘jumping’ or ‘teleportation’ is removed, and a tracking smooth translation provided instead. Therefore, we predict that activation will be observed in the SPL in the ‘teleportation’ displacement trials, but no significant activation will be reported in the SPL when there is smooth pursuit translation. This prediction would therefore suggest that there were visual separation tuned neurons that re-calculate or reset their adaptation state when a reactive saccade is made, whereas when a scanning saccade is introduced for the smoothly translating trials, those same visual separation tuned neurons continue to adapt.

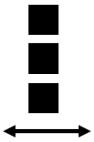
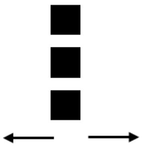
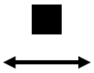
The ‘teleportation’ and translation stimuli are similar in design to conditions 6 and 7 in experiment 1. This was to allow for replication of the results in experiment 1, although the visual stimuli were simplified by removing the cueing circle and dimming events, and the fixation cross was replaced with a third square. Removal of dimming events was felt necessary in case the brief disappearance of one part of the triplet stimulus acted to break adaptation. To replicate the 'teleportation' displacement, the ten pre-determined locations and the leftward, rightward and midline shifts were maintained from experiment 1. The smooth translation stimulus spanned the range of the outer points of the 10 locations. A single translating square was also included to provide a comparison to the displacing and translating triplets. No significant activation in the SPL is also predicted for this translating square for two reasons, firstly because there are no other objects involved in the visual stimuli for visual separation to be calculated with respect to, and secondly because the displacement was smooth, and adaptation was expected.

3.6 fMRI contrasts

This experiment is specifically designed to determine the impact of two different displacement parameters comprising of the teleporting versus smoothly translating displacement of a set of identical triplet squares (see Table 3.6.1). Keeping the same target square triplets in the same configuration allows us to modify the displacement whilst keeping all other parameters constant. The addition of the single translating square will allow us to determine whether the presence of multiple objects contributes to activation in the SPL.

Each of these three conditions will be contrasted with the baseline which consists of three static squares in the same configuration as the triplet squares that displace. This baseline provides a subtractive baseline for the triplet teleporting and triplet translating squares that directly explores the displacement differences because all other parameters are kept the same. An additional contrast that directly pits the triplet teleporting against triplet translating will also be performed.

Table 3.6.1: The conditions of experiment 2 where the single headed arrow depicts the ‘teleportation’ movement, and the double headed arrow represents the smoothly translating movement of that condition. Baseline consisted of three static squares aligned laterally. Activation (✓) under the visual separation hypothesis is only expected in the condition where the visual stimuli teleports to each new location.

Visual Stimuli	Number	Condition	Visual Separation
	0	Triplet static	
	1	Triplet translating	
	2	Triplet teleporting	✓
	3	Single square translating	

3.7 Method

3.7.1 Participants

There were 20 participants who participated in the second experiment. The participants were recruited via advertisements at University of Reading. There were 13 females (7 males) with a mean age of 23.3 years (age range 19 years to 45 years). Ethical approval from the University Board for Research and Innovation (UREC 14.29) was sought and written informed consent was obtained from the participants prior to scanning. The fMRI scans were performed following the University of Reading's Centre for Neuroscience and Neurodynamics (CINN) guidelines and protocols for scanning participants. There were two participants data removed from the ROI analysis due to the omission of a localiser 4D file and one participant data removed from the whole brain analysis due to change in visual stimuli that occurred after the participant was scanned.

3.7.2 Functional localisers

For the second experiment we slightly altered the localiser that we used compared to experiment 1. In that experiment we used *road – flow* contrast when creating the ROI masks alongside the *EML* vs *baseline* contrast. We found that the *road-flow* condition was a high activator of the SPL ROI. Therefore, we kept the *road*, *flow* and *EML* conditions in experiment 2, but did not use the poles condition.

Therefore, the localiser in experiment 2 consisted of four conditions, 1) *road* which consisted of a textured ground plane flow with road edges that wind and weave depicting a forward path and a solid blue sky plane; condition 2) *flow*; (3) *flow* with fixation cross (*flow-fix*) and condition 4) *eye movement localiser* (*EML*) which consists of a white dot that randomly displaces around a black screen (see Figure 3.7.1). However, the road condition had localised SPL activation whereas flow and *flow-fix* had similar activation therefore for continuity with experiment 1, *Road – flow* was used, *flow-fix* was removed from all further analysis.

The visual stimuli that were used for the localiser in experiment 2 were created using Vizard 3.0 (WorldViz). As in experiment 1, participants were pre-taught how to follow the forward trajectory they observed and indicate direction with a joystick for the *road* and *flow* conditions. The *EML* condition only required the participants to follow the white dots movement with saccadic eye movements and fixations.

A block design was again used, and this localiser had 6 repetitions of each condition with a duration of 17 seconds for each block. There was also a *rest* block that consisted of a blank ground plane and grey sky plane and that occurred 6 times. Again, there was a *flash* screen of 1 second duration that would flash to remind the participant whether the next block required them to use the localiser or just their eyes. In half of the *flow* and *road* conditions were 'flipped' to allow the winding and weaving path to go in the opposite direction (left to right, or right to left) to reduce path predictability.

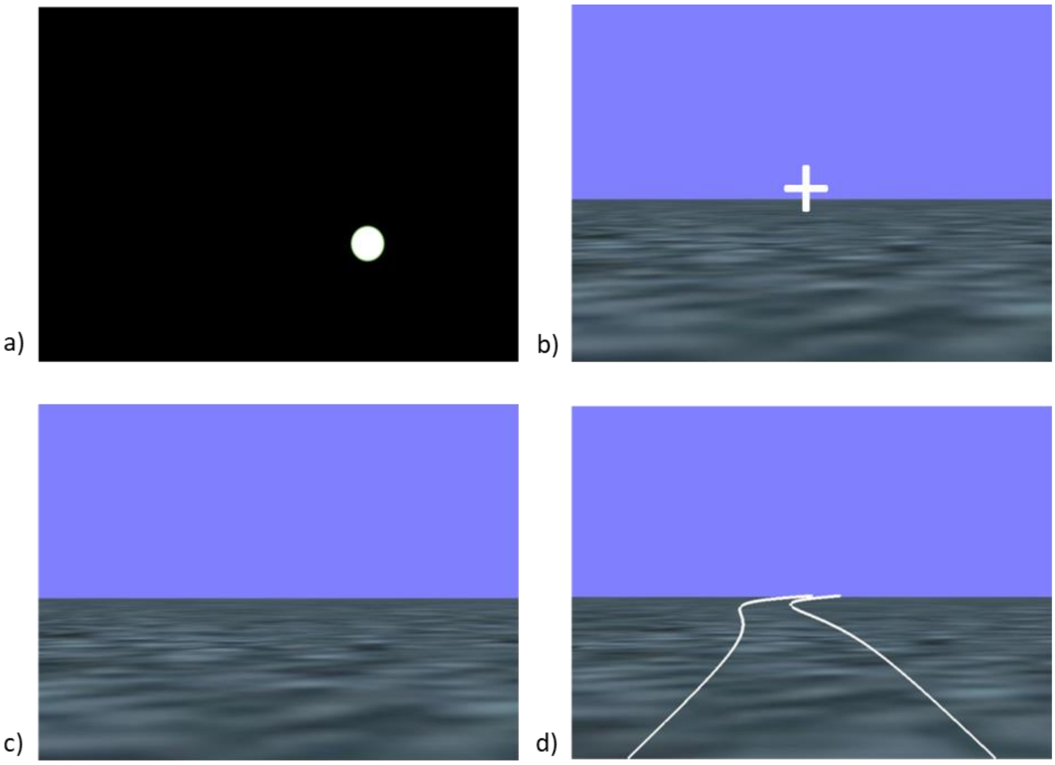


Figure 3.7.1. Conditions used in experiment 2 where (a) the *eye movement localiser* that consisted of a black screen and white dot (*EML*); (b) is the *flow* condition of experiment 1 consisting of the textured ground plane and solid blue sky and a white fixation cross in the middle of the screen (*flow_fix*); and (c) is the same as flow conditions of experiment 1 (*flow*) (d) same as *flow* but with added road edges (*road*) (pictures taken from Inman, (2014)

The road edges in the *road* condition provide elements of stimuli that create visual separation with the remaining elements of the visual stimuli. As stated in experiment 1, the *EML* is used to exclude any voxels that are involved in making saccades from the ROI.

3.7.3 Experimental Stimuli and Design

There were three conditions for experiment 2 that comprised of target square(s). There was no longer a need to include cueing circles or fixation crosses because this experiment was only concerned with the way the target square(s) displaced across the screen. Condition 1 consisted of a triplet of squares that were stacked in a vertical line with an equal distance between them. The centre square would be in the midline of the screen with a square positioned top and bottom. This was the *triplet translating* condition. Condition 2, the *triplet teleporting* condition, comprised of identical visual stimuli which limited the differences between the two conditions to just the displacement. There was also a third condition that consisted of a *single translating square*, which in the event that the *triplet teleporting* condition did not activate the SPL, would be able to provide further information about alternative hypotheses concerning the number of elements of the visual stimuli. (see Table 3.6.1.).

The ten pre-determined locations from the Vandenberghe et al., (2001) study were preserved for the *triplet teleporting* condition to aid replication of the activation in the SPL that was found in conditions 6 and 7 of experiment 1. For the *triplet translating* and the *single translating square*, the range from the two extreme locations of the ten pre-determined locations were used to maintain as many parameters the same as the *triplet teleporting* condition. As the experiment was only concentrating on investigating the displacement type differences, and because the participants were not asked to fixate in one place and attend to another as in some of the conditions of Experiment 1, there was no longer a need for a dimming task to maintain sustained attention. Furthermore, there was a risk that the dimming event could act to break adaptation in a similar way to teleportation of the stimulus. The tracking of the displacement that occurs during the different conditions provided sufficient attention control for this task. Null events were still included in the triplet teleporting condition as part of the constraints that were kept from experiment 1 to ensure that the stimulus shifts were the same. The baseline consisted of three static squares in the same configuration as the *triplet teleporting* and *triplet translating* conditions. This *triplet static* subtractive baseline allows signal change for the other experimental conditions to be calculated in the SPL ROI.

For experiment 2, there were 25 blocks, where the *triplet translating*, *triplet teleporting* and *single square translating* conditions were repeated 6 times. The *triplet static* baseline was repeated 7 times to account for the dephasing double block (Henson, 2007; Josephs, Turner & Friston., 1997). Each block lasted 16 seconds which gave the overall experiment a duration of 400 seconds. The visual stimuli were created using Psychtoolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and run using MATLAB (Mathworks, Inc). The squares that made up each of the different conditions were identical to each other (size = 0.66° x $0.66°^2$ and luminance = 0.09 cd/m^2). The luminance for this experiment was slightly brighter than the visual stimuli in experiment 1. This change was made after piloting to allow the target square(s) to be seen more clearly and is likely to be due to the upgrade of Nordic goggles from those used in experiment 1. Despite the increase in the luminance level, the screen edges continued to be unperceived during the experiment allowing full immersivity in the task. For the *teleporting triplets*, the ten pre-determined locations (-6.38, -4.97, -3.56, -2.15, -0.74, 0.74, 2.15, 3.56, 4.97, 6.38°) used by Vandenberghe et al (2001) study was kept from experiment 1. For the translating conditions, the furthermost locations (-6.38 to 6.38°) were used as the outer edges of the range for the sinusoidal translating displacement.

3.7.4 Procedure

All participants were pre-taught both the localiser and experimental task prior to scanning. This was to ensure that the participant knew what was required of them when they were in the scanner. For the localiser, participants were asked to indicate the heading direction in the *road* and *flow* conditions using a joystick. For the *EML* condition, the participants were required to follow the white dot with saccadic eye movements and fixations as it displaced across the screen. In the experimental tasks, participants were required to fixate on the middle square for all triplet conditions (*teleporting*, *translating*, and *static*) and follow the displacement with their eyes, using saccades or smooth pursuit eye movements as needed. For the *single square translating* condition, participants were required to follow its displacement as it translated across the screen.

Once the participants were confident with what their requirements for the tasks were, written informed consent was taken if they were deemed safe to scan. They were then asked to lie on the scanner table and a 20-channel head coil was then positioned around their head and the Nordic goggles (http://www.nordicneurolab.com) attached to the coil and positioned in front of the participants left eye. The participant would also wear an eye patch on their right eye to eliminate the diplopia that can often be experienced when the Nordic goggles are used binocularly. The goggles were positioned close to the participants eye to allow them to be able to see all four corners of the screen when the scanner room lights were on (the screen edges would effectively disappear when the scanner room lights were switched off during scanning). The goggles would also be adjusted to enable the participant to see the visual stimuli clearly and in focus eliminating the need for participants to wear glasses.

The joystick was fixed on a piece of cardboard that would be partially under the participant to allow it to stay fixed in place. The cardboard and joystick were situated on the right-hand side of the participant and the experimenter checked that it was in a comfortable position that was easily accessible for the participant when they were being scanned. An alarm bell was also given to the participant to enable them to swiftly gain the researchers attention at any point during the scan. Once the participant was positioned correctly and comfortable, the lights in the scanner room were switched off and an intercom was used to communicate with the participant and inform them of each task as they arose and remind the participant of the instructions for that task.

3.7.5 fMRI Data Acquisition

A SIEMENS MAGNETOM Prisma fit 3T MRI scanner was used for this experiment (a scanner upgrade occurred between experiments 1 and 2). The scanner was located in the Centre of Integrative Neuroscience and Neurodynamics at the University of Reading. Nordic Goggles (http://www.nordicneurolab.com) were used to present the visual stimuli to the participants. The joystick used in the Localiser task has already been described in detail in chapter 2.

A 14 second auto alignment scan was performed first that had a TR of 3.15ms, a TE of 1.37ms and a FA of 8 degrees. The voxel size was 1.6 x 1.6 x 1.6mm and there were 128 sagittal slices per slab each with a thickness of 1.6mm. The T1 anatomical scan had a duration of 7 min 30 seconds and a TR of 2400ms, a TE of 2.41ms and the

FA was 8 degrees. There were 224 sagittal slices with a thickness of 0.70mm. The matrix size was 320 x 320 and the FOV = 224mm. The isotropic voxels size was 0.7 x 0.7 x 0.7.

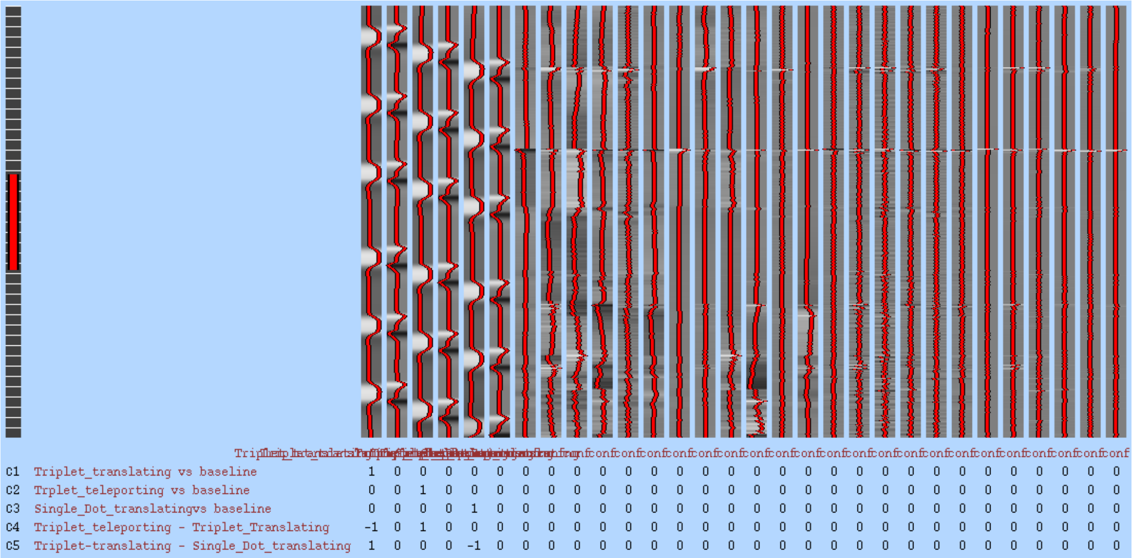
The main EPI for this experiment was 400 seconds in duration and had a TR = 0.972 and TE = 30, FA was 52 degrees. The matrix size was 88 x 88 with a FOV of 210mm. There were 56 sagittal slices with no interslice gap and a thickness of 2.40 mm. There were 348 volumes in total and the multiband factor was 4.

3.7.6 fMRI Data Analysis

3.7.6.1. First Level Analysis

All data processing was completed using FSL (FMRIB's Software Library) version 5.0.9. The pre-processing required plus the GLM were created using FEAT (FMRIB Expert Analysis Tool) (Woolrich, Behrens et al., 2004; Woolrich, Ripley et al., 2001) at the first level initially and then the group level. At the first level a number of pre-statistics steps were applied including motion correction using MCFLIRT (Jenkinson et al., 2002), brain extraction tool (BET) (Smith, 2002) and the spatial smoothing at 5mm FWHM. The registration was to the MNI template.

As with experiment 1 we continued to use standard plus extended motion parameters of GLM which included the Volterra expansion to reduce any residual motion (Lund et al., 2005). No undistortion step using fieldmaps was included in the processing pipeline for this experiment because it proved impossible to process the type of field maps acquired in the upgraded scanner with FSL or other available software. For the GLM, temporal derivatives were added and a high pass filter of 90 was set for each participant. There were three EVs (*triplet translating*, *triplet* *teleporting* and *single square translating*) that were used to model the timecourse (see Design Matrix Figure 3.7.2)



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C1  Triplet_translating vs baseline                1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
C2  Trplet_teleporting vs baseline                 0  0  1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
C3  Single_Dot_translatingvs baseline              0  0  0  0  1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
C4  Triplet_teleporting - Triplet_Translating     -1  0  1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
C5  Triplet-translating - Single_Dot_translating   1  0  0  0 -1  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0  0
```

Figure 3.7.2. Design Matrix for the second experiment detailing the EVs for the 3 experimental conditions and the contrasts that were performed. Temporal derivatives were added alongside a Volterra expansion of the estimated head motion parameters. Note that the design matrix reports a single dot translating, the visual stimuli was a square and not a dot as the name suggests.

3.7.7 Contrast analysis in FEAT

The first level contrasts were applied using FEAT and consisted of three conditions (*triplet translating*, *triplet teleporting* and *single square translating*) versus *baseline* which consisted of three static squares in the same configuration as the triplet displacement conditions. Each of these contrasts allowed investigation into the specific displacement of that condition because the baseline was static and for the triplet conditions containing the same visual stimuli, the only difference between them was the way they displaced. Two additional contrasts were also added, *triplet teleporting – triplet translating* conditions to directly pit the two ways of displacement against each other, and the *triplet translating - single square translating* condition where the single square translating was acting as the baseline for the translating conditions.

We used cluster thresholding throughout this thesis with an initial voxelwise threshold of z =3, and cluster *p* threshold of < 0.05 for all experiments conducted. The cluster thresholding was used for all whole brain analysis at both the first level and the group level. ROI masks were created using the localiser contrasts.

3.7.8 ROI data analysis

The ROI mask were created using the *road – flow* condition and the *EML* vs *baseline* condition, these were the same localiser conditions also used in experiment 1 because they consistently produced activation within the SPL. We used ApplyXFM (part of FLIRT Jenkinson et al., 2002; Jenkinson & Smith, 2001) to resample the MNI standard space to the participants own brain using the highRes2Standard image. Each of the localiser contrasts were then loaded into fslview and their individual thresholds adjusted individually (see table 3.7.3. for threshold numbers). The ROI masks were hand drawn, slice by slice for all voxels that showed activation in the *road – flow* condition and not the *EML* vs *baseline* condition. The Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) was also used to provide a guide for the SPL and only those voxels that were 20% or more likely to be in the SPL included in the ROI mask (see Figure 3.7.4. for an example). Featquery, which is a part of FEAT (Woolrich et al., 2001, 2004) was then used to obtain the mean values of the percentage of BOLD signal change for each of the contrasts in each of the ROI before being analysed in SPSS.

Table 3.7.3. Individual z thresholds for each participant’s data where a ROI mask was created. The masks used the *road – flow* contrast and the *EML* vs *baseline* contrast to identify the voxels that were activated in *road – flow* but were not activated in the *EML* vs *baseline* contrast. Volumes (voxels), mean of % signal change and standard deviations are also displayed for each ROI as well as the peak cluster coordinates within the ROI in mm (standard space) for condition 2 vs sustain (*triplet_teleporting*) in both the left and right hemispheres.

Cond 2 (triplet teleporting vs baseline)									Cond 2 peak cluster coordinates in mm (standard space)					
Participant Number	Road - Flow	EML vs baseline	ROI Volumes (voxels)		Mean		Standard deviation		Left Hemisphere			Right Hemisphere		
	Z	Z	Left	Right	Left	Right	Left	Right	x	y	z	x	y	z
1	No localiser files													
2	No localiser files													
3	3	4	No ROI	37	No ROI	0.06	No ROI	0.13	No ROI			11.1	-51.3	73.1
4	3	3	57	80	0.75	-0.03	0.68	0.49	-31.1	-59.7	59.3	15	-57.5	60.3
5	2	3	No ROI	1	No ROI	0.15	No ROI	0.00	No ROI			30.7	-52.4	69
6	1	4	11	14	0.07	0.24	0.41	0.53	-31.2	-58.3	63.2	16.5	-56.5	71.2
7	3	3	7	9	0.08	0.12	0.14	0.08	-24	-55.4	58.6	21.7	-57	60.5
8	3	4	7	45	0.08	-0.57	0.15	0.27	-27.5	-50.7	61.1	13.1	-53.4	61.1
9	3	4	1	3	0.64	1.42	0.00	0.83	-36.1	-46.4	48.6	16.1	-56.8	69.7
10	3	2	137	48	-0.01	-0.19	0.32	0.22	-43.1	-42.2	54.2	23.2	-53.1	53.8
11	3	4	21	15	-0.02	0.06	0.10	0.07	-36.5	-54.7	65	33.6	-53.7	66.8
12	3	4	128	35	0.45	0.19	0.45	0.15	-44.7	-44.6	53.9	29.8	-47.2	50.5
13	4	3	32	80	-0.48	-0.06	0.37	0.22	-21.3	-56.3	67.4	17.5	-58.7	64.6
14	3	3	24	44	0.32	0.31	0.21	0.30	-16.3	-54.9	63.8	19.7	-48.5	69.7
15	3	1	24	164	0.30	0.20	0.43	0.35	-19.1	-59.4	59	16.7	-56	68.3
16	3	3	49	49	-0.06	0.25	0.25	0.18	-15.8	-55.8	60.1	11.1	-52.9	71.2
17	3	3	48	92	0.17	0.30	0.16	0.29	-22.4	-53.7	61.9	20.9	-47.9	75.9
18	2.5	2.5	224	135	-0.45	0.05	1.14	0.54	-28.9	-58	65.7	36.4	-43.2	65.1
19	2	3	24	2	0.28	0.43	0.16	0.09	-26.4	-58	49.7	23.4	-55.5	68.3
20	2	2	5	47	0.11	0.55	0.36	0.45	-33.9	-49.6	66.3	27.7	-58.5	65.9

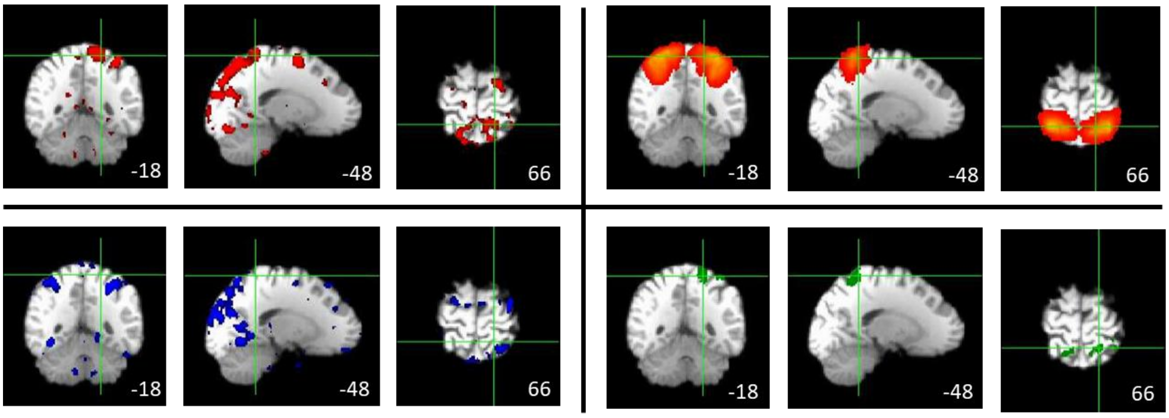

Figure 3.7.4. Example of individual participant data highlighting the contrasts used to create the ROI mask for experiment 2. Top left panel: *road* minus *flow* contrast (threshold min 3, max 5). Bottom left panel: *EML* vs *baseline* contrast (threshold min 2, max 5). Top right panel: Unthresholded map of SPL atlas from Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) Bottom right panel: ROI mask

3.8 Results

3.8.1 Teleportation condition replication

In conditions 6 and 7 in experiment 1 we were able to see high BOLD signal for both conditions. This experiment included a *triplet teleporting* condition consisting of three squares that displaced under the same parameters as conditions 6 and 7 in experiment 1. In the whole brain analysis, activation was observed bilaterally in this condition in the SPL at coordinates x20, y-60, z60 and x-20, y-60, z60 and a successful replication was possible (see Figure 3.8.1.).

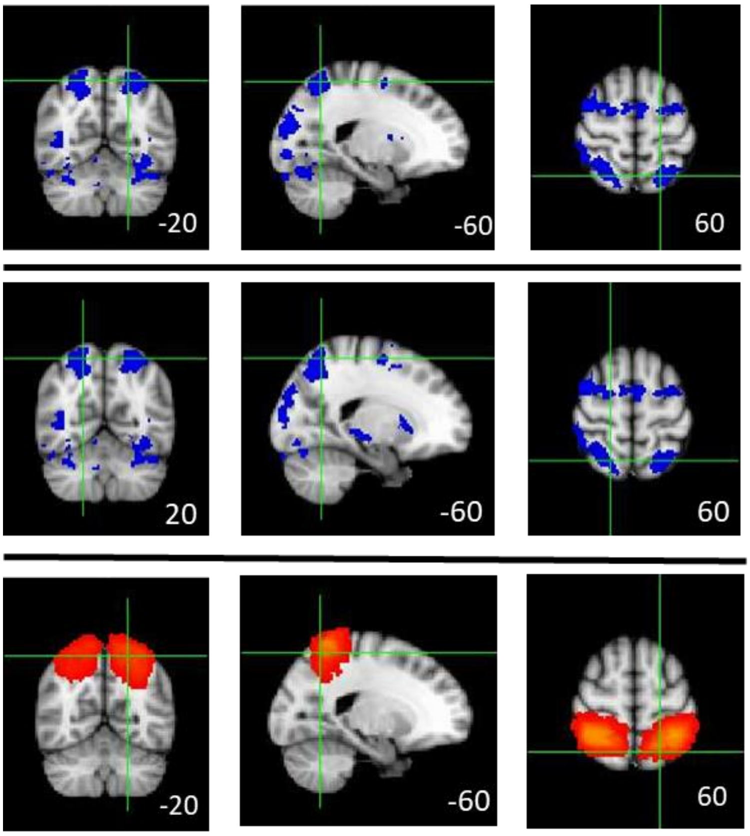

Figure 3.8.1. Top: Activation shown bilaterally in the SPL area for the *triplet teleporting* condition versus *baseline* (3 static squares) at coordinates for the left hemisphere; middle: activation shown for the *triplet teleporting* condition versus b*aseline* at coordinates for the right hemisphere, both with the cluster voxelwise threshold z=3, with a cluster p threshold of <0.05; bottom: Unthresholded map of SPL atlas from Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006).

3.8.2 Translating conditions

The translating conditions were used to determine if removing the ‘teleportation’ effect would produce reduced activation, consistent with adaptation in visual separation tuned neurons in the SPL. The two translating conditions in this experiment consisted of *a triplet translating* condition and a *single square translating* condition. As predicted, in the whole brain analysis there was no activation observed in the SPL at coordinates x-20, y-60, z60 for either condition which provides support for adaptation of separation tuned neurons occurring once the ‘teleportation’ effect has been removed (see Figure 3.8.2.).

To further verify the difference in SPL due to the type of stimulus movement, the contrast: *triplet teleporting – triplet translating* was created (see Figure 3.8.3.) and bilateral activation was observed at coordinates x20, y-60, z 60, and x-22, y-60, z56. The ROI analysis showed that there was a much higher percentage signal change in SPL in the *triplet teleporting* condition compared to the slightly negative percentage signal change observed in the translating conditions (see Figure 3.8.4. showing all three conditions).

A paired t-test was performed on the ROI BOLD signal change data to see if there was a significant difference between the *triplet teleporting* condition and *triplet translating* condition. This t-test confirmed that there was a significant difference between teleportation and translating displacement *t* (17) = 2.949, p =0.009 furthering support for our interpretation that the translating conditions produce adaptation in visual separation tuned neurons. The negative percentage signal change in the other two conditions were not significantly different from zero, *triplet translating t* (17) = -.813, p=.427, *single square translating t* (17) = -.157, p=.877.

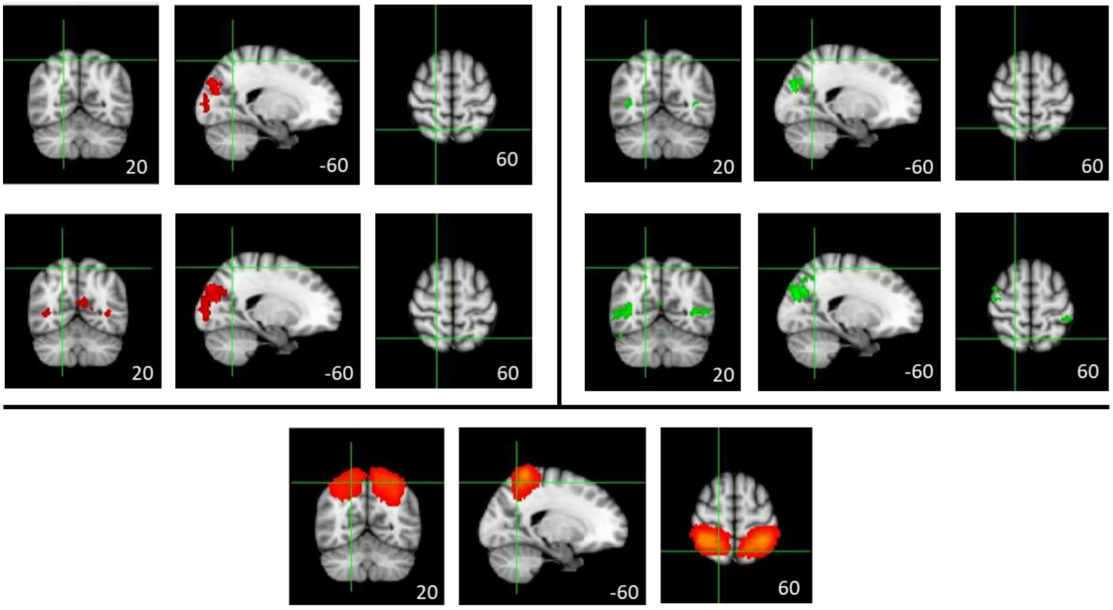

Figure 3.8.2. Top left : No activation in the SPL area at coordinates for the *triplet translating* condition vs *baseline* (3 static squares) at cluster threshold z=3 voxelwise; middle left: No activation in the SPL area at coordinates for the *triplet translating* condition vs *baseline* (3 static squares) at a more liberal cluster threshold z= 2.3 voxelwise; top right: No activation in the SPL at coordinates for the *single square translating* condition versus baseline (3 static squares) both conditions at cluster threshold z=3 voxelwise; middle right: No activation in the SPL at coordinates for the *single square translating* condition versus baseline (3 static squares) both conditions at a more liberal cluster threshold z= 2.3 voxelwise. All conditions had a cluster p threshold of <0.05; bottom: Unthresholded map of SPL atlas from Harvard-Oxford Cortical Structural Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006).

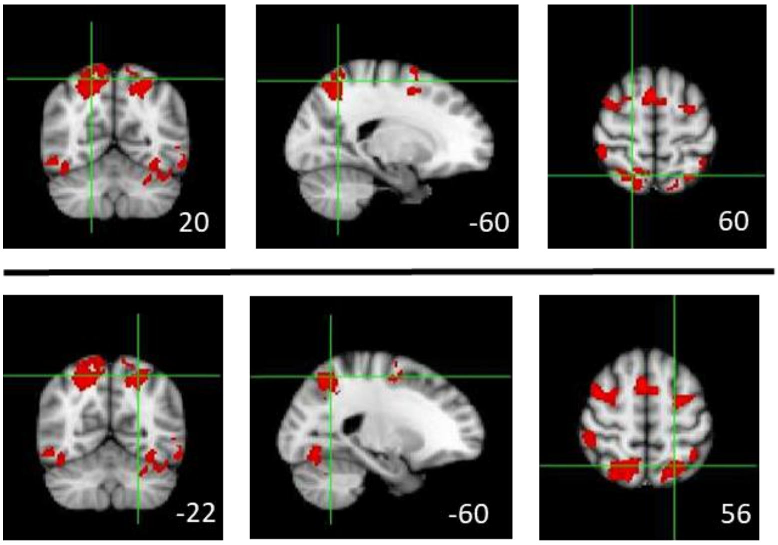

Figure 3.8.3. Top: The contrast *Triplet_teleporting – triplet_translating* produced activation in right hemisphere (x20, y-60, z60) and Bottom: activation was also produced in the left hemisphere at coordinates (x-22, y-60, z56). Both contrasts were at cluster threshold z=3, with a cluster p threshold <0.05.

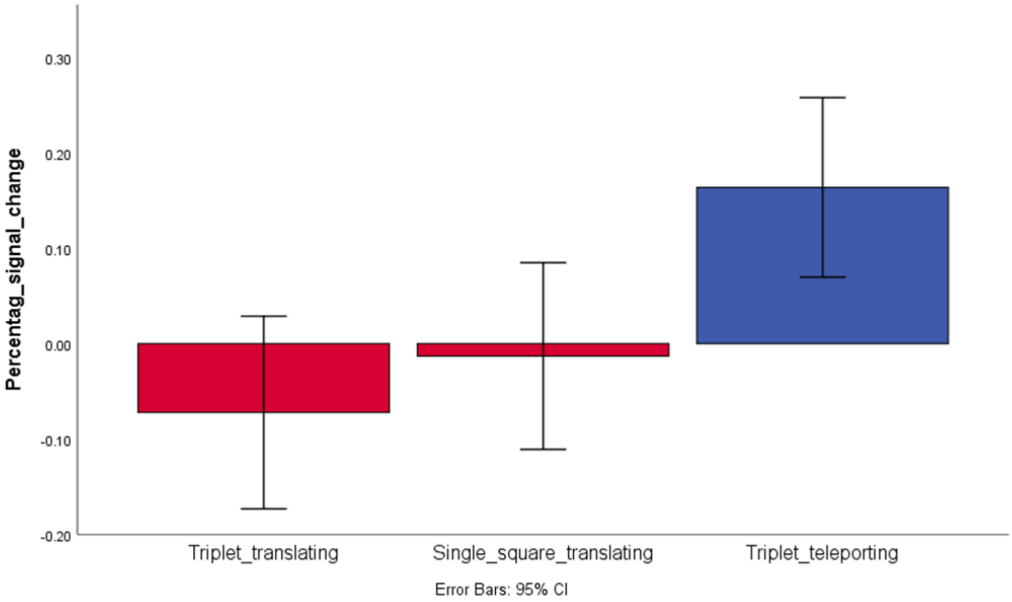

Figure 3.8.4. The two translating conditions (triplet and single square) are depicted in red and show a negative percentage signal change in the ROI compared to the *triplet teleporting* conditions shown in blue. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

3.9 Discussion

Conditions 6 and 7 of experiment 1 produced results that required further exploration, and this was accomplished here. These two conditions followed the same constraints as the other conditions of experiment 1 including displacement parameters, dimming events and null events. However, the visual stimuli included additional elements (two target squares) compared to the other conditions and the cueing circle(s) in these two conditions changed to show the participants where a dimming event would occur, whereas in conditions 1 – 5 the cueing circle prompted the participant where to fixate, either overtly or covertly.. One big difference between conditions 6 and 7 and the rest of the conditions of experiment 1 was that all of these multiple elements moved in unison (including the fixation cross) which we had predicted would eliminate visual separation between the multiple elements as they displaced. We proposed that the way the visual stimuli was displacing could account for the activation we had found in the SPL. The results of experiment 2 showed that by recreating the 'teleportation' effect successfully and observing no SPL activation for the two translating conditions provided support for our proposal that when the visual stimuli displaced in smooth translation, adaptation would occur in the visual separation tuned neurons of the SPL. Whereas, when the displacement appears to 'jump' or 'teleport' to a different location then adaptation is broken, and a re-calculation of the visual stimuli takes place at each new location.

The *single translating square* condition from experiment 2 as well as the single teleporting square condition 1 from experiment 1, provide further support of our visual separation hypothesis with neither of the two conditions activating SPL despite changes in displacement that showed activation differences when multiple objects were present. The displacement changes are not important when there is a single, solitary object because without multiple objects, visual separation cannot be calculated.

As expected, there was activation in the SPL ROI observed for the *triplet teleporting* condition. This replicated the results that were also observed in experiment 1 and was consistent with our suggestion that the 'teleportation' effect makes visual separation to be re-calculated at each new location. In contrast to this condition, both the *triplet translating*, and *single square translating* conditions did not activate the SPL ROI providing evidence that adaptation occurred in these conditions. Returning to the visual separation hypothesis, the number of objects used (in this experiment: 1 and 3) did not change the adaptation effect observed for the translating conditions despite there being multiple visual separations between the objects, because when they displaced in unison on a smoothly translating path adaptation still occurred. This therefore provides support for the visual separation hypothesis.

Looking back at experiment 1's results now that clarification of the teleportation/adaptation effect has been obtained, lower BOLD activation was observed in the static conditions (conditions 0 (baseline), 2 and 4). Whereas there was activation in the conditions that 'teleported' to each new location (conditions 3, 5, 6 and 7) and apart from condition 1 (single square teleporting) which had no significant activation in the ROI. The teleportation appears to influence the BOLD signal that was observed during these conditions in the task, apart from condition 1.

The single square teleporting was the only moving condition in experiment 1 that did not produce any activation in SPL even though it was teleporting to the different locations, the same as was witnessed in the other teleporting conditions. The dimming event was also possible during this trial and the participants were anticipating a dimming event occurring at random times throughout the trial, therefore their level of attention would be similar to an overt condition (e.g. condition 5) where they were asked to attend to the target square, where all dimming events would occur (apart for condition 6 where the dimming event could occur in the upper square, leaving the lower square as unimportant; and condition 7 where the dimming event could occur in either the upper or lower squares). The lack of activation in the single teleporting square condition (condition 1) and the *single translating square* condition provides further support for the visual separation hypothesis due to the very nature of their singularity. With the absence of other objects there was no requirement to calculate the visual separation and visual angle. The fact that ‘teleportation’ was present in condition 1 shows that ‘teleportation’ by itself is not a sufficient condition to activate SPL.

The shifting spatial attention hypothesis proposed by Vandenburghe and colleagues (2001) would expect significant activation in the single teleporting condition because the participants attention was still shifting at each new location, however a low BOLD signal occurred that was not significantly different from baseline. In the *single square translating* condition, participants were required to follow the target square as it moves laterally across the screen and back. The nature of the eccentricity of the square was predictable and therefore adaptation was expected. The participants attention did not have to shift between locations as was evident in the teleportation conditions, their attention remained upon the target square, but the translating nature ensured that attention continued equally along a path where the only shift in direction occurred at the edge of the range at both the left and right extremes. After the initial change in direction at either end became predictable adaptation could occur throughout the trial. These single square conditions provide evidence in contradiction to the shifting spatial attention hypothesis.

The displacement changes within this experiment could be considered a potential confound due to the type of eye movements that are required for each displacement. The scanning saccades likely to be initiated when tracking the translating objects are different to the reactive saccades that are expected to be used during the ‘teleportation’ displacement. This could therefore suggest that the SPL activation that we observed was due to saccades and fixations, while smooth pursuit does not activate SPL. However, condition 1 of experiment 1 still required saccades and fixations and there was minimal activation for this condition in the SPL, making the change in eye movements unlikely to be responsible for the activation in the SPL.

Another potential alternative explanation for our pattern of activation would be to propose that SPL is suppressed during smooth pursuit eye movements. This was not explicitly investigated in this experiment but Kimmig et al., (2008) and Ohlendorf et al., (2010) both had conditions incorporating smooth pursuit together with a change in visual separation and both of these achieved activation in the SPL, so this rules out the suppression explanation.

As mentioned earlier whilst Kimmig et al., (2008) did produce activation in the SPL for a smooth pursuit stimulus that had no comparable visual separation between them, Ohlendorf et al., (2010) did not activate the SPL when there was smooth pursuit of objects that had no differences in displacement. The results of the translating conditions of experiment 2 corroborate Ohlendorf et al., (2010) findings.

In conclusion, this experiment neatly illustrates that the shifting spatial attention hypothesis can be refuted and provides further evidence that the visual separation hypothesis can be the proposed function of the SPL. However, further investigation into the visual separation hypothesis is needed to ensure its robustness as the explanation of the function of the SPL brain area. An additional fMRI experiment that incorporated the information gained from experiments 1 and 2 and further expansion upon this area is needed. Specifically, the next experiment will take these questions and attempt to answer them by exploring relative and absolute visual separation.

Chapter 4 – Experiment 3

4.1 Overview of experiments 1 and 2

In experiment 1, conditions 3 and 5 (which consisted of a fixed element and displacing elements viewed covertly and overtly, respectively) produced activation in the SPL. This could be as a result of shifting of attention of the displacing object or due to changes in visual separation between fixed and displacing stimuli. However, condition 1 in experiment 1 refuted the shifting spatial attention hypothesis proposed by Vandenberghe et al., (2001) because whilst the visual stimuli and attention continued shifting spatially under the same parameters as conditions 3 and 5, it did not activate the SPL. The lack of activation argues strongly against the proposal that the function of the SPL involves shifting of attention. The solitary object in condition 1, however, supported the visual separation hypothesis because multiple objects are required to calculate visual separation against and therefore non-significant activation in the SPL is consistent with the visual separation hypothesis.

Experiment 1 also produced strong activation in the SPL for conditions 6 and 7. The visual stimuli in these two conditions including the fixation cross would displace across the screen under the same parameters as conditions 1 ,3 and 5. The unison displacement was expected to produce low BOLD signal and were included in the experiment to test a divided attention hypothesis where the BOLD signal under this hypothesis would be expected to be higher for the stimuli that encouraged participants to divide their attention the most (condition 7). No significant activation was expected under the visual separation hypothesis because all elements of visual separation moved together therefore visual separation remained constant. The high BOLD signal for both conditions were at odds with the visual separation hypothesis.

Experiment 2 explored the displacement differences between visual stimuli and determined that the visual stimuli appeared to ‘jump’ or ‘teleport’ across the screen each time they displaced to a new location. By removing the ‘jumping’ aspect of displacement we removed the SPL activation that was observed when the shifting or ‘jumping’ stimuli were reinstated. This provided encouragement for the notion that adaptation played a part when the stimuli displaced with smooth translation. However, when the same stimulus displacement appeared to ‘jump’ to each new location the visual separation tuned neurons responded by re-calculating the visual separation as if it was novel. The adaptation effects in the translating conditions of experiment 2 resolved the apparent problem in experiment 1.

Whilst it could be argued that it was replacing displacement with translation that reduced the SPL activation in experiment 2 compared to experiment 1, it is worth noting the results of Ohlendorf et al., (2010) who used smooth translating dots of varying numerosity with a fixation point in all conditions. These conditions, similar to conditions 3 and 5 of experiment 1 consisted of a fixed element and a moving/displacing element. Ohlendorf et al., (2010) observed activation in the SPL particularly when the dots moved smoothly away from the fixed point, showing that the visual separation between these elements could have produced activation without the presence of displacement. Furthermore, condition 1 of experiment 1 also demonstrates that displacement on its own is not responsible for SPL activation.

This brings us to experiment 3 which will be an exploratory look at the effects of different components of visual separation in SPL: interobject distance and visual angle and whether changes to these components individually could be responsible for the function of the SPL or whether a combination of the two is needed.

4.2 Frame of references and coordinate systems

Frames of references can be used to monitor changes within an environment. Karn, Moller, & Hayhoe, (1997) described three types of frames of reference: retina-centred, head or body centred and object-centred which they investigated in terms of location memory. Changes that are object-centred are also known as exocentric or allocentric and these types of reference frames relate to using objects as the point of reference irrespective of, or independent of the observer, such as providing directions for an item using the objects around or near as its reference points (Karn et al., 1997).

A coordinate system is also required to measure differences within the frame of reference. That coordinate system will use points of reference as well as a reference direction to provide details of any changes that are made (Wolbers & Wiener, 2014). The cartesian coordinate system that plots coordinates on an x, y and z axis (Volkwyn, Gregorcic, Airey & Linder, 2020) is commonly used in reporting graphical data. However, the polar coordinate system has been used to plot retinotopic maps in the brain using polar angle and eccentricity (Henriksson, Karvonen, Salminen-Vaparanta, Railo, & Vanni, 2012), and matches more closely the properties of the visual system. Therefore, a polar coordinate system will be used in this thesis to describe interobject distance and visual angle.

4.3 Changes in visual separation – interobject distance and visual angle

Visual separation thus far in this thesis has referred to distances between objects and visual angle as a combined entity. Breaking this down into smaller components would provide further understanding of visual separation which in turn can provide clues to the function of the SPL. If we look at visual separation in a simple form with two objects e.g., dots, and position them a set distance from each other, then that will provide an interobject distance, the distance between one object relative to another object. Interobject distance and the retinal distance between the images of the two objects create a one-for-one mapping as long as the observer keeps their eyes and head still and the distance between the observer and the objects remain constant. This distance between objects (also termed exocentric distance) has been researched alongside egocentric distances where the distance relates to between person and object rather than between objects themselves (Matsushima, Vaz, Cazuza, & Ribeiro Filho, 2014; Norman, Adkins, Pedersen, Reyes, Wulff, & Tungate, 2015).

Visual angle, as with interobject distances is often investigated with egocentric properties where the visual angle between the observer's fovea and the object is calculated (Vaillancourt, Haibach, & Newell, 2006), but here we investigate visual angle in the image plane of the retinal image. Visual angle can also be obtained using a coordinate system between the objects (Aznar-Casanova, Matsushima, Da Silva, & Ribeiro Filho, 2008). This visual angle will change with displacement of some of the visual stimuli when other elements are stationary or displace in a different direction on most occasions.

Experiment 3 will be exploring the components of visual separation: interobject distance and visual angle, by creating stimuli that can examine these different components individually or in combination with each other. Interobject distance relates to the distance between the objects in the visual stimuli. Visual angle relates to the angle of the objects on the retinal image. To do this a polar coordinate system will be used to determine the changes in both interobject distance and visual angle where the observer’s fovea is treated as the origin, and the central stimulus is maintained on the fovea (see Figure 4.3.1a).

Exploring these two components of visual separation both individually and as a combination will allow us to determine whether the SPL function is concerned about interobject distance or visual angle or a combination of the two. A change in interobject distance without a change in visual angle can occur when an object displaces away from another object creating a change in interobject distance, but the visual angle remains the same. Using a polar coordinate system with a vertical reference direction, the displacement changes occur without a change in visual angle when both objects are on the same axis following the reference direction (see Figure 4.3.1b). For changes in visual angle when interobject distance remains unchanged, the object location would need to change (see Figure 4.3.1c) with the vertical reference direction providing the visual angle changes. For objects where one remains static and the other displaces creating a larger interobject distance this will also create a visual angle change (see Figure 4.3.1d).

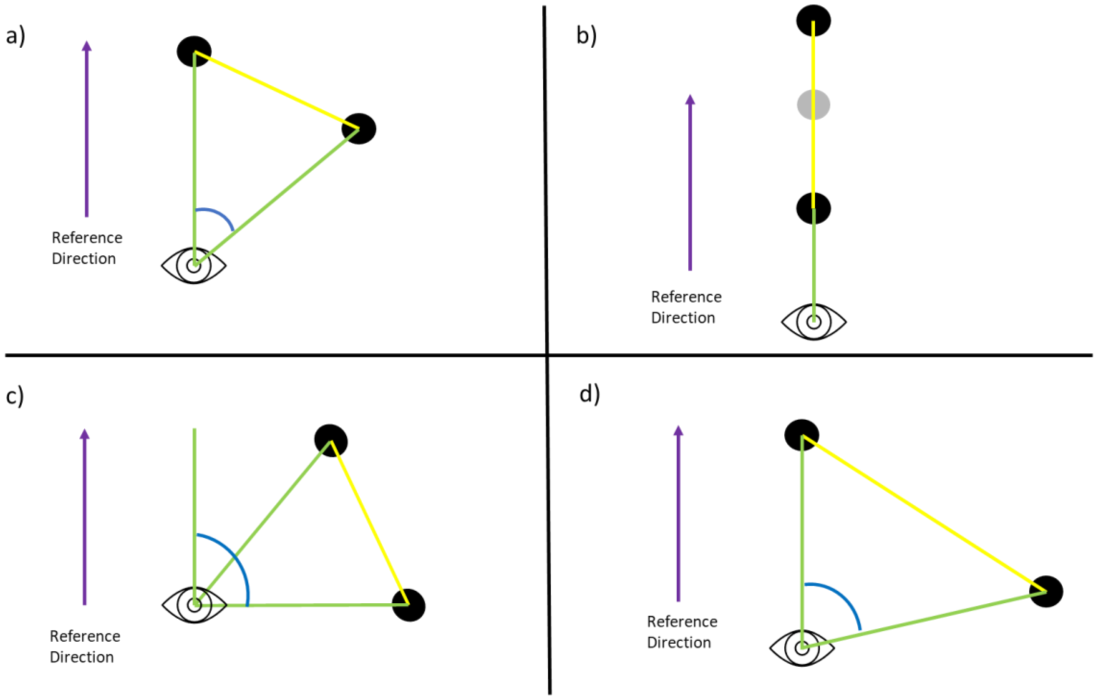

Figure 4.3.1. Using two dots as an example to show the different variations of interobject distance and visual angle either with individual changes or as a combination. In all scenarios the eye symbol represents the fovea, the reference direction is vertical (purple arrows), the interobject distance is depicted by the yellow lines, the polar coordinate system depicted by the green lines with the fovea as the origin and the light blue curve showing the visual angle. *a)* This shows two dots with a fixed interobject distance and visual angle; *b)* shows a change in interobject distance where the lower dot remains static and the grey dot shows the upper dots previous position, no change to visual angle because the displacement occurred on the same axis following the reference direction; *c)* The interobject distance is the same as in *a)* but in a new location therefore changing the visual angle (light blue curve shows the visual angle in the new location); *d)* A change in visual angle and interobject distance compared to *a)*.

For experiment 3 the participants will have their head, body and eyes fixed still relative to the stimulus. Due to the nature of the fMRI experiment the head and body are refrained from motion and for this experiment the participants eyes will be fixated on a central dot keeping the head, body, and eyes relative to the visual stimulus. This therefore makes a head- and body centred as well as allocentric frame of reference irrelevant. Keeping the eyes of the observer on a fixed point will make the retinotopic frame of reference the same as the allocentric (the computer screen for example), therefore whatever visual stimulus is on the screen is also what is on the retinotopic frame of reference. However, this would not be the case if a participant moved their eyes.

4.4 Hypotheses and predictions

By breaking visual separation down into its components, we can further determine whether both activate the proposed visual separation neurons in SPL or whether there is a preference for one type or another. Taking the visual angle as a separate entity, are changes to interobject distance and visual angle important for the SPL or does one surpass the other?

We have already described in this thesis that visual separation requires multiple objects, it cannot occur with a single solitary object. The visual separation hypothesis predicts that because a change in the visual separation between multiple objects when one object is stationary or when multiple objects displace in different directions creating a change in the separation between objects, we would expect activation in the SPL ROI. It would be ideal for a study to be able to easily separate the changes in interobject distance from changes in visual angle. However, to create visual stimuli that keeps these two elements of visual separation mutually exclusive whilst maintaining the same configuration proved a challenge that we were unable to master. Using multiple objects to create visual stimuli to further expand upon the two previous experiments of this thesis was possible where we could use identical stimuli for each of the conditions. We were able to create visual stimuli that could be separated into 4 properties: a change in both interobject distance and visual angle between a central element and the remaining objects; a change in interobject distance between a central element and the remaining objects but no change in visual angle; a change in visual angle only between a central element and the remaining objects; and no change in interobject distance or visual angle between a central object and the remaining objects. For the visual separation hypothesis, we would predict that for the conditions that have a change in interobject distance will activate the SPL, whereas for the condition where there are no changes in interobject distance or visual angle we would not expect any activation in the SPL.

4.5 fMRI contrasts

The conditions where activation in the SPL is expected are those where there is a change in the interobject distance between the stimuli. The displacement of multiple objects that create this visual separation has already been shown to activate the SPL ROI in experiment 1 and 2, when there is a displacement between a static object and displacing objects. When there is no change in interobject distance or visual angle then no significant activation in the SPL is predicted. For one condition, the displacement changes the visual angle between the remaining objects without a change in the distance between the objects, this condition will allow us to explore if visual angle as a separate element of visual separation is important to the proposed visual separation tuned neurons or if the change of interobject distance between the objects is also required.

4.6 Method

4.6.1 Participants

Experiment 3 was conducted with the same participants as experiment 2 in a separate scanner run, before experiment 2. For details, please see chapter 3. One participant was excluded from the ROI analysis because of the absence of localiser 4D data file and three of the participants were excluded from experiment 3 analysis because of an absence of 4D data file for one; and two participants had an incorrect baseline which excluded them from the baseline contrast, but they were included in any analysis that did not include the baseline contrasts.

4.6.2. Functional localisers

This third experiment utilised the same functional localisers that were used in experiment 2, please refer to chapter 3 for details.

4.6.3 Experimental stimuli

Experiment 3 utilised five conditions that each consisted of 5 dots in a 2-1-2 formation for all five conditions (see Figure 4.6.3). The use of dots rather than squares was necessary for condition 4 because the use of squares would have introduced additional complications in creating some of the stimuli. In all conditions, participants were asked to fixate on the central dot throughout all trials and track the central dot with their eyes if it moved.

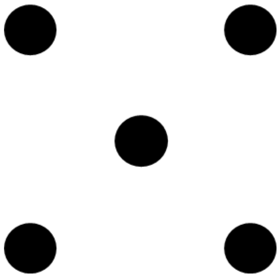

Figure 4.6.3. The 2-1-2 dot formation of the visual stimuli used for all stimuli in experiment 3

Condition 0 (*baseline*) consisted of 5 dots in the 2-1-2 formation that remained static throughout the trial. Condition 1 (*translating_5*) consisted of 5 dots in the same 2-1-2 formation, these dots translated across the screen using the same distance range as was used for the translating conditions for experiment 2. The interobject distance and visual angle between the dots remain constant for both these conditions while the dots smoothly translated across the midline of the screen maintaining the interobject distance and visual angle between the dots (see Figure 4.6.4). To match the motion energy of individual dots across all the experimental conditions, the total excursion of moving dots in the other conditions were matched to that in condition 1. Condition 2 (*CD4UpDown*) consisted of 5 dots again in the same 2-1-2 formation, however, the central dot remained static and the remaining 4 outer dots translated smoothly up and down. There was a clear change in interobject distance between the outer dots and the central dot and a change in visual angle between the central dot and each of the outer dots because the outer dots travel either further away or closer to the central dot (see Figure 4.6.5).

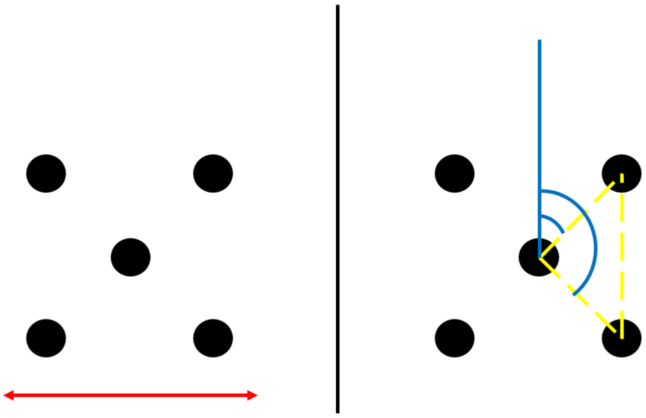

Figure 4.6.4. Left: *translating_5* condition consisting of the 2-1-2 formation, red arrow depicts smooth translation of all 5 dots; Right: Using three dots to explain the visual separation components (yellow dashed line). The polar coordinate system using the fovea as origin (participants fixate on the central dot throughout the trial) where the vertical blue line shows the reference direction, and the blue curves shows the visual angle between two objects. No change in interobject distance and visual angle for this condition.

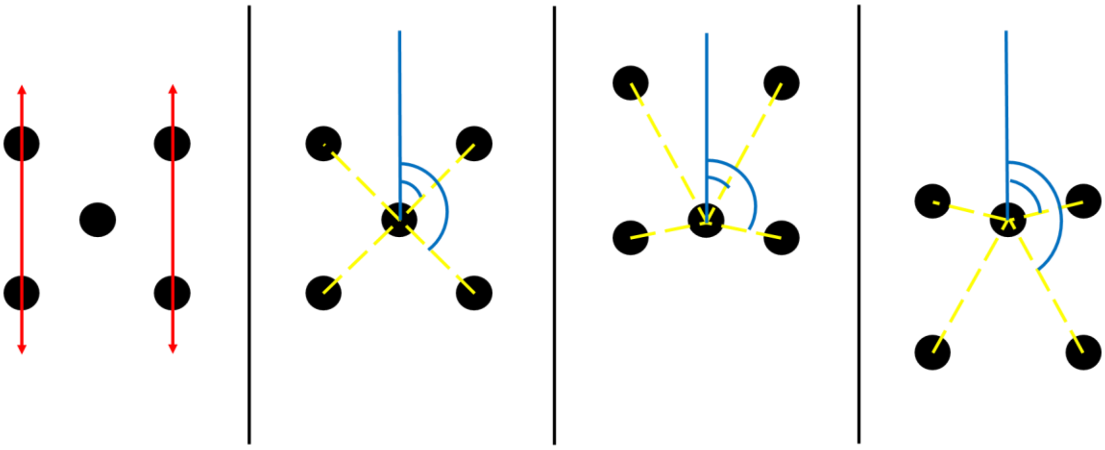

Figure 4.6.5. First panel: *CD4UpDown* condition where the central dot is static, and the red arrows depict smooth translation up and down for the outer four dots. In the second, third and fourth panels, the yellow dashed line depicts the interobject distance between the central dot and the outer dots, the vertical blue line shows the reference direction, and the blue curves show the visual angle of two objects. These three panels show example positions that

the outer dots would be located at during the trial. In this condition there is a change in interobject distance and visual angle.

Condition 3 (*CD4Expand*) consisted of the same 5 dots in a 2-1-2 formation this time the central dot remained static throughout the trial and the outer 4 dots expanded out and in during the trial. This expansion and contraction created only a change in interobject distance between both the central dot and the outer dots (see Figure 4.6.6.).

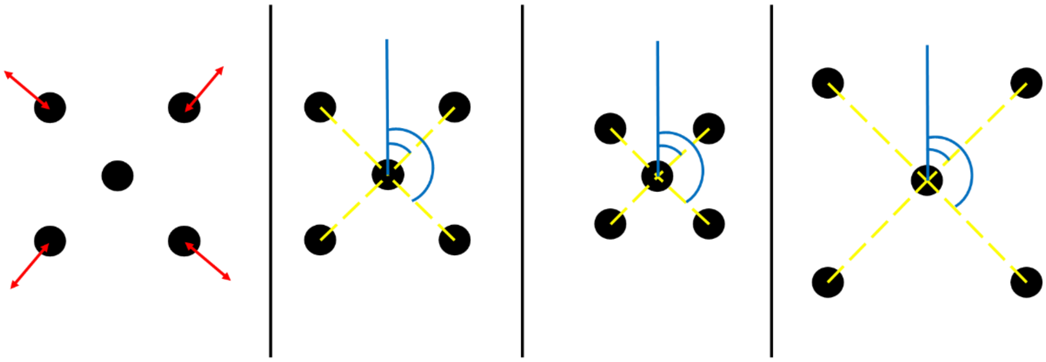

Figure 4.6.6. First panel: *CD4Expand* condition where the central dot remains static and the outer dots expand out and back in towards the central dot (red arrows depict translation). In the second, third and fourth panels, the yellow dashed line depicts the interobject distance between the central dot and the outer dots, the vertical blue line shows the reference direction, and the blue curves show the visual angle of two objects. These three panels show example positions that the outer dots would be located during the trial. In this condition there is a change in interobject distance only.

Condition 4 (*CD4Rotate*) consists of 5 dots that have the initial formation of 2-1-2, as before the central dot remains static but this time the remaining 4 outer dots rotate around the central dot (no direction reversals). If squares had been used, as in Experiment 2, the visual distance between the squares would be complex because there would be a change of visual separation from each of the four corners of a square (see Figure 4.6.7). With wanting to simplify the visual stimuli and to reduce unnecessary variables the use of dots would remove the awkwardness and provide the centre of the dot as the point of which interobject distance would be measured. In this condition there are only changes in visual angle between the central dot and the outer dots, there are no interobject distance changes.

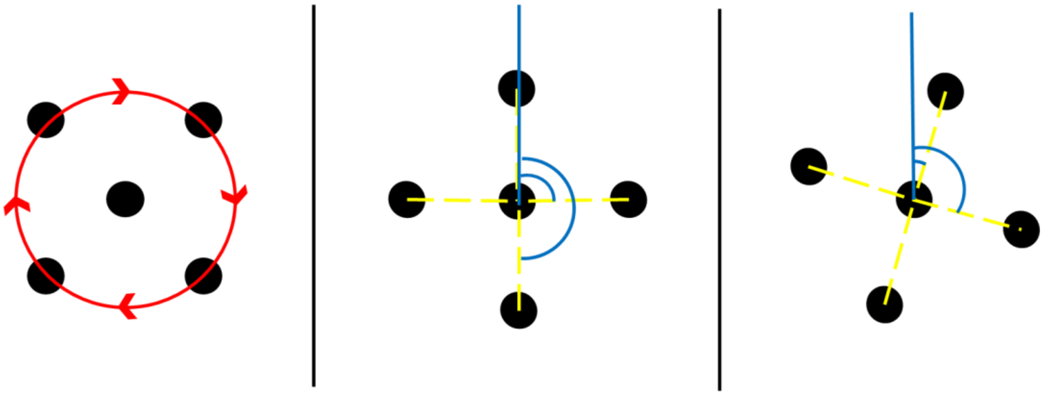

Figure 4.6.7. First panel: *CD4Rotate* condition where the central dot remains static and the outer dots rotate around the central dot at a fixed interobject distance (red arrows depict translation); In the second and third panels, the yellow dashed line depicts the interobject distance between the central dot and the outer dots, the vertical blue line shows the reference direction, and the blue curves show the visual angle of two objects. These two panels show example positions that the outer dots would be located at during the trial. In this condition there is a change in visual angle only.

4.6.4. Experimental design

In experiment 3 there were 31 blocks and *translating_5*, *CD4UpDown*, *CD4Expand* and *CD4Rotate* were each repeated 6 times and baseline was repeated 7 times, this was for the dephasing double block (Henson, 2007; Josephs et al., 1997). The blocks each lasted 16 seconds which made the total duration for the experiment, 496 seconds. Psychtoolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) was again used to create the visual stimuli and it was run using MATLAB (Mathworks, Inc). The visual stimuli used to create each of the conditions including the baseline were identical and comprised of 5 individual dots (size = 0.66° of visual angle, full width and height was 6.6° of visual angle and luminance was 0.09 cd/m^2). There were some variations to the movement of each condition. For the *translating_5* condition the distance the stimuli moved was 12° (6° to the left and 6° to the right). The dots translated at 3° per sec (48° travelled in each 16 sec block)[8]. In the *CD4UpDown* and *CD4Expand* conditions the average speed (3° per sec) was assigned to the four dots that moved within the visual stimuli to match the *translating_5* condition, this also allowed us to match the total distance travelled as well. However, the excursion size was smaller in these two conditions resulting in more excursions required to balance the average speed and total distance travelled in the *translating_5* condition: resulting in 4.5 cycles in the *CD4UpDown* condition and 8 cycles in the *CD4Expand* condition. The *CD4Rotate* condition held a constant speed of 3° per sec and one dot would travel 1.5 times around the full circumference during the 16 sec block. Again, it was a priority to ensure that the screen edges were unperceived during this experiment.

4.6.5 Procedure

Experiment 3 followed the same procedure as in experiment 2 (see chapter 3 for more details). Specifically, for experiment 3, participants were pre-taught to fixate on the central dot throughout all trials, and in the case of the *translating_5* condition, track the central dot as that condition translated, however for all other conditions the central dot remained in a fixed central position.

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[8] This is the average speed reported, there are some variations to the acceleration and deceleration of movement over a cycle due to the nature of the sinusoidal function that controlled the motion.

4.6.6 fMRI Data Acquisition

Details regarding fMRI data acquisition can be found in chapter 3. The main EPI for experiment 3 followed the same parameters as experiment 2, although the number of scans in the 4D series was different (408 in this experiment) and it lasted 397 secs. In terms of running order of the experimental EPI scans, experiment 3 was before experiment 2.

4.6.7. fMRI Data Analysis

4.6.7.1. First Level Analysis

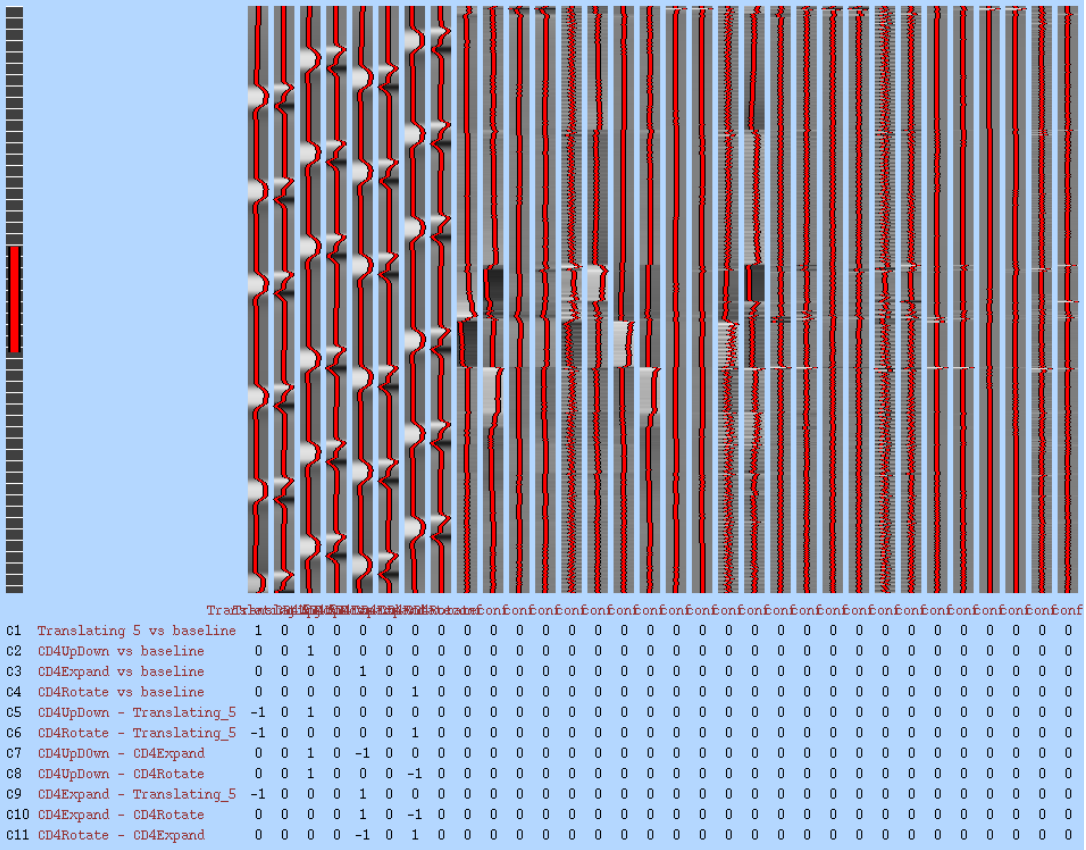
All data processing that was required for experiment 3 was completed using FSL (FMRIB's Software Library) version 5.0.9. This included pre-processing that was used both at the first level and the group level. As with experiments 1 & 2, a number of pre-statistics steps were performed which included motion correction using MCFLIRT (Jenkinson et al., 2002), brain extraction tool (BET) (Smith, 2002) and spatial smoothing was set to 5mm FWHM. MNI template was used for registration again for this experiment.

The same standard plus extended motion parameters of the GLM including Volterra expansion to reduce residual motion (Lund et al., 2005) was used for this experiment. Fieldmaps were also not acquired in this experiment for the same reasons as detailed in chapter 3 relating to the scanner upgrade. Temporal derivatives were added to the GLM as well as a high pass filter set to 90 for each participant. There were four EV's (*Translating_5*, *CD4UpDown*, *CD4Expand* and *CD4Rotate*) used to model the timecourse (see Design Matrix Figure 4.6.8)

4.6.8 Contrast analysis in FEAT

FEAT was used for all first level contrasts which consisted of the four experimental conditions (*Translating_5*, *CD4UpDown*, *CD4Expand* and *CD4Rotate*) versus *baseline* (5 static dots). Each of these conditions including the baseline were comprised of the same 5 dots in a 2-1-2 formation. These contrasts allowed investigation into the effects of changes to interobject distance and visual angle on brain activation in the four conditions where movement occurred against the static nature of the baseline. The remaining contrasts were created to explore the separate components of visual separation. This was to determine if there was a preference for the proposed visual separation neurons within the SPL ROI that may activate when either one or both are present.

Cluster thresholding was used for this experiment with an initial voxelwise threshold of $z = 3$, and cluster p threshold of < 0.05. This clustering was used for all whole brain analysis that is presented in this chapter at both first level and group level, however, when a condition has a lack of activation in the SPL a more liberal threshold with an initial voxelwise threshold of $z = 2.3$, and cluster p threshold of < 0.05 is used. The localiser contrasts were used to create the ROI masks.



C1	Translating 5 vs baseline	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C2	CD4UpDown vs baseline	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C3	CD4Expand vs baseline	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C4	CD4Rotate vs baseline	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C5	CD4UpDown - Translating_5	-1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C6	CD4Rotate - Translating_5	-1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C7	CD4UpDOwn - CD4Expand	0	0	1	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C8	CD4UpDown - CD4Rotate	0	0	1	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C9	CD4Expand - Translating_5	-1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C10	CD4Expand - CD4Rotate	0	0	0	0	1	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C11	CD4Rotate - CD4Expand	0	0	0	0	-1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Figure 4.6.8. Design matrix for experiment 3 detailing the four experimental conditions and contrasts. Temporal derivatives were added alongside a Volterra expansion of the estimated head motion parameters. The baseline used in the first four contrasts consisted of 5 static dots in the 2-1-2 formation.

4.6.9. ROI definition

The localiser contrasts that were used to create the ROI masks were the identical *road – flow* and *EML* vs *baseline* contrasts that were used in experiment 2 (see chapter 3 for more details). ROI volumes and peak cluster coordinates for *CD4UpDown* condition can be seen in Table 4.6.9.

4.7 Results

Each of the four conditions were contrasted with *baseline* at an individual first level before being combined at group level to create a group analysis average.

4.7.1. Whole brain analysis

The *CD4UpDown* condition had the static central dot which participants fixated on provided a fixed point to which the change of interobject distance would be established between the central dot and the four outer dots. The change in visual separation (primarily the changes in interobject distance, but also the changes in visual angle that were present) predicted, under the visual separation hypothesis, activation in the SPL. Activation was indeed observed bilaterally at and near the coordinates (x20, y60, z60 and x-20, y-60, z60) in the SPL ROI highlighting that interobject distance and visual angle have an effect on SPL (Figure 4.7.1.).

Table 4.6.9. Each participants' individual z thresholds used to create the ROI masks used for analysis. The masks were constructed by overlaying the *EML* vs *baseline* contrast on the *road – flow* contrast and identifying the voxels that were activated in *road – flow* but not *EML* vs *baseline*. Volumes (voxels), mean of % signal change and standard deviations for each ROI are displayed alongside the peak cluster coordinates in mm (standard space) for the *CD4UpDown* condition in both the left and right hemispheres.

Cond 2 (*CD4UpDown* vs baseline)									Cond 2 (*CD4UpDown*) peak cluster					
Participant Number	Road - Flow	EML vs baseline	ROI Volumes (voxels)		Mean		Standard deviation		Left Hemisphere			Right Hemisphere		
	Z	Z	Left	Right	Left	Right	Left	Right	x	y	z	x	y	z
1	No Localiser Files													
2	No Localiser Files													
3	3	4	No ROI	37	No ROI	0.73	No ROI	0.41	Not included for condition vs baseline contrasts due to an incorrect baseline					
4	3	3	49	83	0.08	0.10	0.40	0.35	-21.4	-52.8	70.7	17.9	-56.1	58.8
5	3	3	No ROI	2	No ROI	0.49	No ROI	0.30	No ROI			30.3	-53	68.1
6	1	4	16	17	1.03	0.48	0.67	0.39	-31.5	-59	65	21.6	-51.5	74.4
7	3	3	1	12	0.50	0.48	0.00	0.18	-23.4	-56.8	59.6	15	-58.3	63.4
8	3	4	9	42	0.15	0.37	0.10	0.20	-38	-36.5	47.9	13.3	-55.2	66.9
9	3	4	1	2	0.11	1.03	0.00	0.46	-36	-46.2	49.4	13.6	-57.5	69.7
10	3	2	131	53	0.16	0.13	0.21	0.21	-23.6	-51.6	70.2	23.7	-56.3	57.2
11	3	4	20	17	0.40	0.54	0.12	0.11	-33.8	-58.7	59.3	38.9	-50.9	64.8
12	3	4	127	33	-0.31	-0.04	0.42	0.18	-36.1	-38.2	54.1	35.9	-44	59.9
13	4	3	28	82	0.24	0.04	0.94	0.15	-28.4	-47.1	71.2	15.3	-51.2	74.4
14	3	3	20	43	0.31	0.51	0.12	0.20	-15.8	-53.1	66.6	25.1	-46.4	63.2
15	3	1	23	167	0.46	0.58	0.18	0.44	-18.9	-58.5	58.8	35.7	-39.9	60.4
16	3	3	49	48	0.63	0.43	0.40	0.22	-27	-56.4	67.5	12.9	-52.8	69.8
17	3	3	50	83	0.68	0.23	0.38	0.44	-23.5	-51.6	67.4	22.5	-52.1	61.9
18	2.5	2.5	216	128	-0.03	0.56	0.63	0.56	-24	-55.4	70.9	34.9	-44.5	64.6
19	2	3	21	4	0.55	0.91	0.19	0.09	-25.9	-56.4	49.9	24	-56.7	68.8
20	2	2	3	44	0.25	0.58	0.11	0.23	-17.8	-59.7	64.9	19.6	-57.7	63.6

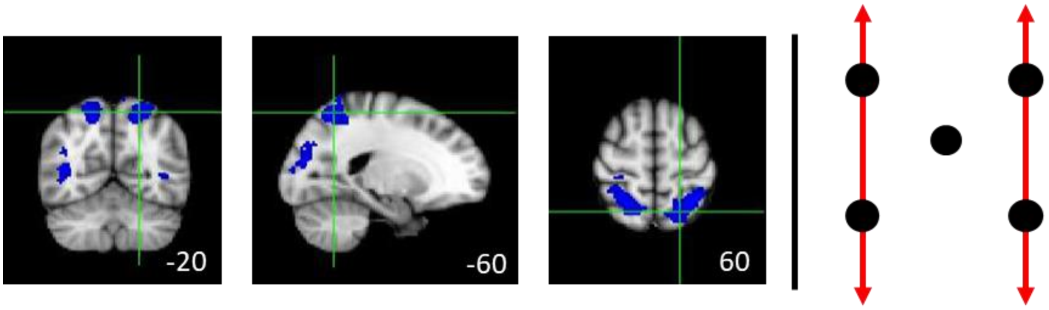


Figure 4.7.1. Whole brain analysis of the *CD4UpDown* condition which consisted of 5 dots in a 2-1-2 configuration (where the central dot remained fixed and the outer 4 dots displaced (depicted by the red arrows) in a up and down trajectory) versus *baseline* (5 static dots in the

same 2-1-2 formation). Activation occurred bilaterally in the SPL at coordinates (x-20, y-60, z60 and x20, y-60, z60).

The *CD4Expand* condition also has a static central dot where in this condition the four outer dots expand and contrast towards and away from the central dot. Whilst this condition does not provide any changes to visual angle between the central dot and the four outer dots, there is a change in interobject distance, and we therefore predicted activation in the SPL for this condition. Surprisingly, this was not the case and no activation was observed in the SPL at coordinates at a voxelwise threshold of z=3 or at a more liberal voxelwise threshold of z=2.3 with a cluster p threshold <0.05 (see Figure 4.7.2.).

The *CD4Rotate* condition had the static central dot and the outer dots would rotate around the dot at a fixed distance. This therefore produced no changes to interobject distance but there were changes in the visual angle relative to the fovea (central dot). This condition would allow us to determine if visual angular changes had an impact on the SPL. Activation was observed in the SPL in the left hemisphere only near coordinates x-20, y-60, z60 (see Figure 4.7.3.) and the extent of the activation was smaller than for CD4UpDown. Nonetheless, this result suggests that changes in visual angle are also important for SPL.

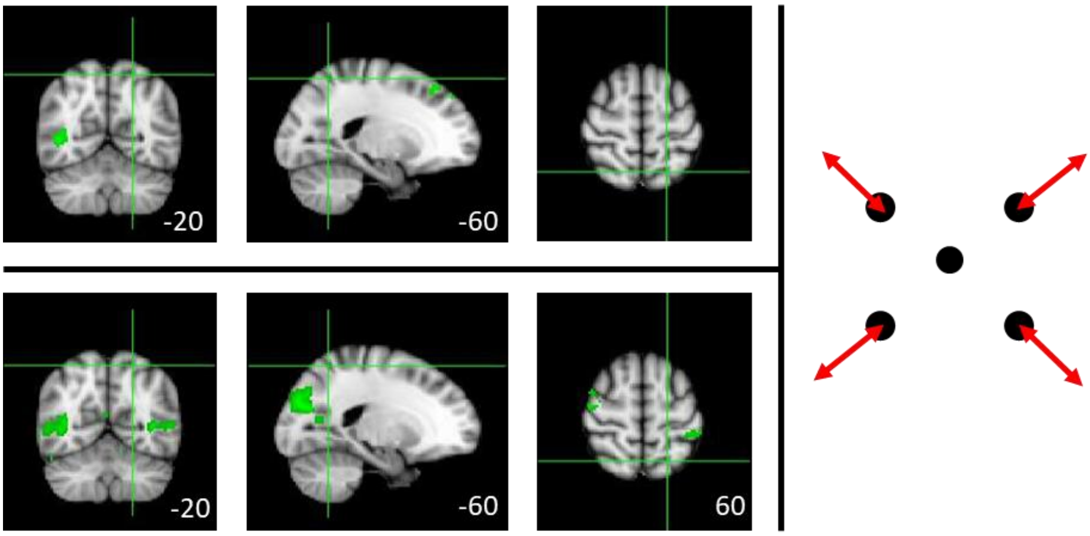


Figure 4.7.2. Whole brain analysis of the *CD4Expand* condition which consisted of 5 dots in a 2-1-2 formation (where the central dot remained fixed and the outer 4 dots (depicted by the red arrows) expand and contract away from the central dot) versus *baseline* (5 static dots in the same 2-1-2 formation). No activation was observed at coordinates at voxelwise threshold z=3 (top) or voxelwise threshold z=2.3 (bottom) Cluster p threshold <0.05 for both.

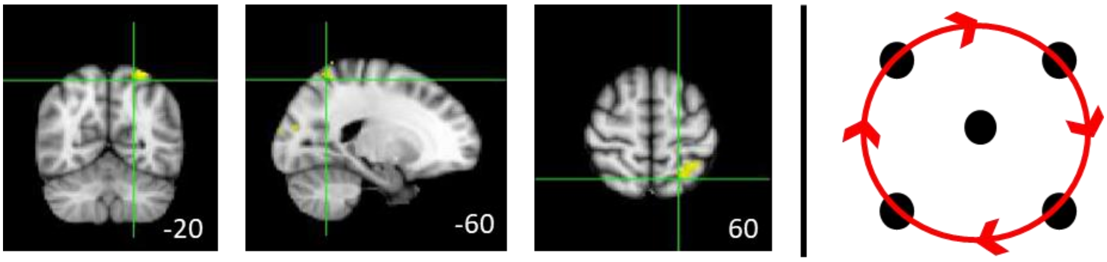


Figure 4.7.3. Whole brain analysis of the *CD4Rotate* condition which consisted of 5 dots in a 2-1-2 formation (where the central dot remained fixed and the outer 4 dots displaced (depicted by the red arrows) around the central dot at a fixed length) versus *baseline* (5 static dots in the same 2-1-2 formation). Activation occurred near the SPL at coordinates in the left hemisphere.

The *translating_5* condition is the only condition where the central dot moved along with the outer dots. They all smoothly translated, in unison, laterally across the screen, in the same way as the *triplet translating* and *single square translating* conditions in experiment 2. Based on the results of experiment 2 and Ohlendorf et al., (2010), we were confident that there would be no significant activation for this condition, however, in this condition, activation occurred in the left hemisphere at and near the coordinates x -20, y -60, z 60 (see Figure 4.7.4). These results are at odds with the findings from experiment 2.

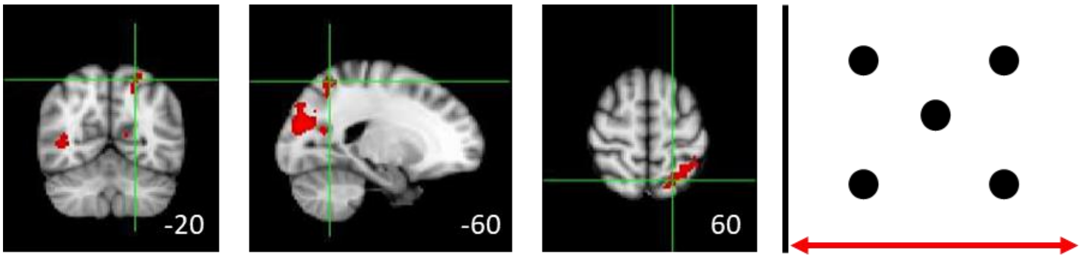


Figure 4.7.4. Whole brain analysis of the *Translating_5* condition which consisted of 5 dots in a 2-1-2 configuration (all 5 dots translating laterally depicted by the red arrow) versus *baseline* (5 static dots in the same 2-1-2 formation). Activation is in the left SPL at coordinates.

4.7.2. ROI Analysis

The contrasts used for the ROI analysis were the *road - flow* and *EML* versus *baseline* contrasts from the Localiser scan used in experiment 2. Featquery was then used to calculate the percentage of BOLD signal change for each condition. The conditions that had a change in interobject distance with or without changes in visual angles were expected to have a higher BOLD signal change. Experiment 3 as an exploratory study is also looking at whether visual angles individually or in combination with interobject distance produce a higher BOLD signal change in the SPL ROI.

In condition *CD4UpDown* there was a clear change in interobject distance and visual angle between the central dot and the outer dots and had the highest percentage signal change compared to the other conditions, (see Figure 4.7.5) with the right hemisphere producing higher signal change than the left hemisphere. This condition highlights that the components of interobject distance and visual angle combined are important to the proposed visual separation tuned neurons in the SPL. The *CD4Expand* condition was also predicted to activate the SPL due to changes in interobject distance, but a negative percentage BOLD signal change was actually produced. This result casts doubts on the value of isolated interobject distance changes being responsible for activation in the SPL. The *CD4Rotate* condition produced a higher percentage signal change in the right hemisphere compared to the left hemisphere. This condition had no change in interobject distance, but it did have changes in visual angle. This suggests that visual angle does have a role in the activation of the SPL, whereas when combined with changes to interobject distance as in the *CD4UpDown* condition, stronger activation in the SPL is observed. The *translating_5* condition had a higher percentage signal change in the left hemisphere compared to the right and was the only condition that this occurred. There were no changes in interobject distance or changes to visual angle and therefore the expectation for this condition was for it to follow the results that were observed in experiment 2 and produce a lack of activation, however, activation did occur and has provided conflicting results to experiment 2.

To investigate the responses to the visual stimuli for each condition further one sample t-tests were performed to see where there was significant activation above zero. Each of the four conditions involved movement that would highlight interobject distance or visual angle changes, a combination of the two or no changes at all (see Table 4.7.6.). *CD4UpDown* was significantly different from zero in both left and right hemispheres and *CD4Rotate* was significantly different from zero in the right hemisphere. These results suggest that the combination of changes to interobject distance and visual angle produced significant activation in both hemispheres and changes to visual angle in isolation produced signification activation in the right hemisphere. The negative signal change observed in the right hemisphere for *CD4Expand* was not significantly different from zero, and the unexpected activation for the translating stimulus was close to but failed to reach significance.

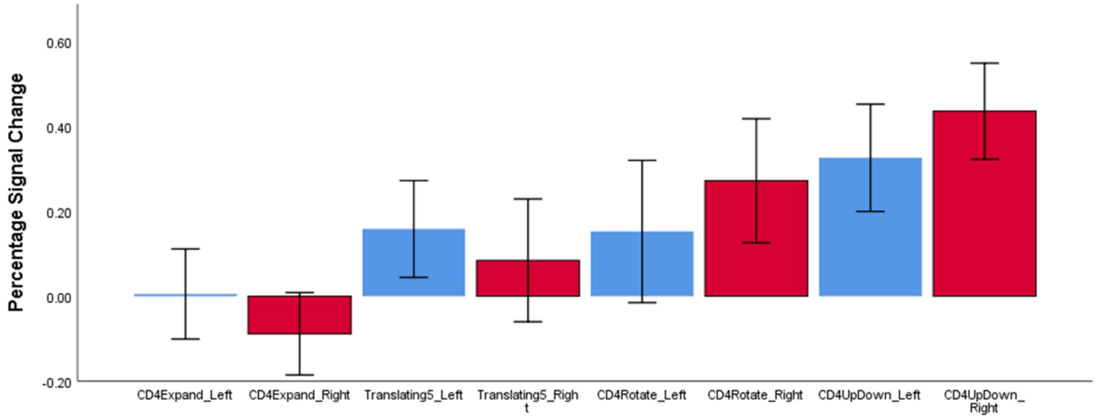


Figure 4.7.5. Percentage BOLD signal change for the four experimental conditions in experiment 3 with the left hemisphere shown in blue and the right hemisphere in red. Error bars are adjusted for repeated measures (Field, 2018; Loftus & Masson, 1994) and show 95% confidence intervals.

Table 4.7.6. One sample t-tests on BOLD signal change in the ROI for each of the conditions separated by hemisphere

						95% Confidence Interval of the Difference	
Condition	**Hemisphere**	**t**	**df**	**Sig (2-tailed)**	**Mean Difference**	**Lower**	**Upper**
CD4Expand	Left	0.063	16	0.950	0.005	-0.169	0.179
	Right	-1.270	16	0.222	-0.089	-0.237	0.059
Translating_5	Left	1.990	16	0.064	0.159	-0.010	0.328
	Right	0.925	16	0.369	0.085	-0.109	0.278
CD4Rotate	Left	1.399	16	0.181	0.153	-0.079	0.384
	Right	2.865	16	0.011	0.272	0.071	0.474
CD4UpDown	Left	4.372	16	0.000	0.327	0.168	0.485
	Right	6.343	16	0.000	0.437	0.291	0.583

A repeated measures 2 (Hemisphere: Left, Right) x 4 (Condition: *CD4Expand, Translating_5*, *CD4Rotate*, *CD4UpDown*) ANOVA was also conducted. Missing data in individual hemispheres was mean substituted, and sphericity was assumed. The main effect for hemisphere was not significant (*F* (1, 16) = .065, *p* = .802, ηp^2 = .004). The main effect for condition was significant (*F* (3, 48) = 9.971, *p* <.001, ηp^2 = .384 and the interaction between hemisphere and condition was also significant (*F* (3, 48) = 5.644, *p* = .002, ηp^2 =.261). To further explore the main effect of condition and in particular the *CD4UpDown* condition and whether it was a significantly stronger activator compared to either *CD4Rotate* or *translating_5* conditions, a special contrast (IBM SPSS Statistics 25 Command Syntax Reference) was performed. This special contrast confirmed that *CD4UpDown* (changes in interobject distance and changes in visual angle) was significantly stronger in activating the SPL than either *CD4Rotate* (that had changes in visual angle only) and *translating_5* (that had no changes in either interobject distance or visual angle) (*F* (1,16) = 15.042, *p* = .001). A special contrast (IBM SPSS Statistics 25 Command Syntax Reference) was also performed to determine whether *CD4Rotate* had significantly stronger activation than the *translating_5* condition, where it was found not to be significant (*F* (1,16) = .763, *p*=.395) which indicates that the changes in visual angle only were not significantly stronger than moving stimuli where no changes in interobject distance or visual angle occurred. A special contrast (IBM SPSS Statistics 25 Command Syntax Reference) was also performed to ascertain whether the *CD4UpDown* condition activated more strongly than the *CD4Rotate* condition and it was found to be very close to significance (*F* (1,16) = 4.268, *p*=.055), which suggests that changes in both interobject distance and visual angle were a stronger activator than changes to visual angle alone. Finally, a post-hoc observation on Figure 4.7.5. is that for the right hemisphere the gradient between the condition with the strongest activation and the condition with the least activation is steeper, which indicates that the right hemisphere has greater selectivity for visual separation properties. This would need to be confirmed in future experiments.

A series of 2 (hemisphere: left, right) x 2 (condition: in a variety of configurations) repeated measures ANOVAs were conducted to provide further clarity on the significant interaction found in the 2 x 4 repeated measures ANOVA reported above (see Table 4.7.4 which only reports the relevant interaction, not the main effects). The reason for the interaction in the 2 x 4 ANOVA, which is supported by the pattern of significant vs non-significant interaction in Table 4.7.7 is that for the *CD4UpDown* and *CD4Rotate* conditions, the right hemisphere has higher activation than the left hemisphere, whereas in contrast, for the *translating_5* and *CD4Expand* conditions the left hemisphere has higher activation than the right. Note that higher referred to here is not indicative of strength relative to zero activation, but rather it could be viewed as relative to the largest negative number plotted in Figure 4.7.5.

Table 4.7.7. 2 x 2 ANOVA interactions to further explore the interaction found in 2 x 4 ANOVA.

Condition Interaction	**F**	**D of F**	***p***	**ηp^2**
CD4Rotate vs CD4UpDown	0.028	(1,16)	0.868	0.002
CD4Expand vs translating_5	0.100	(1,16)	0.756	0.006
CD4UpDown vs translating_5	5.772	(1,16)	0.029	0.265
CD4UpDown vs CD4Expand	6.559	(1,16)	0.021	0.291
CD4Rotate vs CD4Expand	7.716	(1,16)	0.013	0.325
CD4Rotate vs translating_5	13.725	(1,16)	0.002	0.462

4.8 Discussion

Whilst experiment 3 was primarily an exploratory study looking at more complex visual stimuli when visual separation is separated into two components: interobject distance and visual angle, it was still predicted that changes in the interobject distance component of visual separation would activate the SPL ROI. This was indeed the case in the *CD4UpDown* condition where there were changes in both interobject distance and visual angle, producing strong bilateral activation in the SPL. The *CD4Expand* condition had changes to interobject distance only but was still predicted to activate the SPL however, this did not occur. We shall discuss this in more detail below. The *CD4Rotate* condition had changes in visual angle only and produced activation in the left hemisphere of the SPL. The *translating_5* condition which had no changes to the interobject distance or visual angle was expected to follow the results of experiment 2 which observed a single square and triplet squares translating and no significant activation in the SPL was produced. In contrast to these results from experiment 2, the *translating_5* condition did activate the left SPL in the whole brain analysis (though not significantly in the ROI analysis), and this will be explored further.

4.8.1. Absolute change versus relative ratios

The *CD4Expand* condition comprised of a fixed element (central dot) and moving elements (four expanding and contrasting outer dots). The fixed central point and the moving outer elements provided changes in interobject distance whilst the visual angle remain constant. Two dots have been used to produce changes in interobject distance earlier in this thesis when one dot remains static or moves in a different direction to the second displacing dot. Experiment 3 comprised of more complex visual stimuli, and the lack of activation in *CD4Expand* could be explained by ratios, more specifically if the SPL is sensitive to detecting changes in the ratios of multiple visual angles when more complex stimuli are presented. For the *CD4Expand* condition the ratios between all visual angles, and also between all interobject distances, remain fixed (the size of the dots remained constant as well) and that produced no significant activation in the SPL. The interobject distances changed (they got further apart from and closer to the central dot), but the ratio of the distances compared to the central dots and the outer dots remained the same (they all changed at the same rate). This fixed ratio means there was absolute expansion and contraction. On the other hand, the *CD4UpDown* condition produced strong bilateral activation and here the ratios between visual angles and between interobject distances all changed. Extending the absolute/relative concept to the *CD4Rotate* condition, there was relative rotation compared to the reference direction of a polar coordinate system and this produced activation in the left hemisphere. These findings are consistent with the idea that the SPL is selective to relative changes in interobject distance and/or visual angle. This proposal would need to be tested in further experiments.

Looking back over earlier findings in this thesis the changes that were present, when stimuli consisted of two objects, was a change in interobject distance. Defining those changes as absolute or relative is not feasible in the same way as it is with more complex stimuli such as those in experiment 3. The proposal that relative/ratio level changes are important for SPL is evident in more complex stimuli such as condition CD4UpDown where the relative changes produced a change of shape (there was no perceived change of shape for the CD4Expand condition). One possibility that could link the findings in this chapter to those in earlier chapters is that the stimuli made up of two objects used in earlier parts of this thesis could be interpreted as a change in the length of a line, which might be equivalent to the shape distortion that is perceived in more complex stimuli when the ratios between visual separations change.

4.8.2. Number of visual separations

For the *translating_5* condition, adaptation was expected to occur as it did when there were 1 and 3 objects translating in unison. What had changed between these conditions that could affect the results and produce weak unilateral activation in the SPL? Note that given it only trended towards significance in the ROI analysis this result requires replication, but we discuss it here on the basis that it was a true effect. Each of the conditions were displacing within the same location range, in a smooth translation. Could numerosity explain the difference in activation? Potentially yes, but not necessarily the number of objects that create the visual stimuli but the number of visual separations (interobject distance) that increases as the number of objects increase. Where numerosity relates to the actual number of items within a group, other visual features that make up that group such as the total edge length are also affected when numerosity is changed (Harvey, Klein, Petridou, & Dumoulin, 2013).

These changes could involve the visual separation (interobject distance) that will in turn increase as numerosity increases. Indeed, visual separation could arguably be processed by the brain prior to numerosity because numerosity cannot be changed without changing the interobject distance between the objects, while the other way round is possible. As the numerosity increases the visual separation (interobject distance) increases at a higher rate suggesting that a small increment in numerosity creates a larger increase of visual separation, which could overwhelm the proposed visual separation tuned neurons and break adaptation that can occur when there are fewer number of objects and therefore a possible visual separation decrease too (see Figure 4.9.1.).

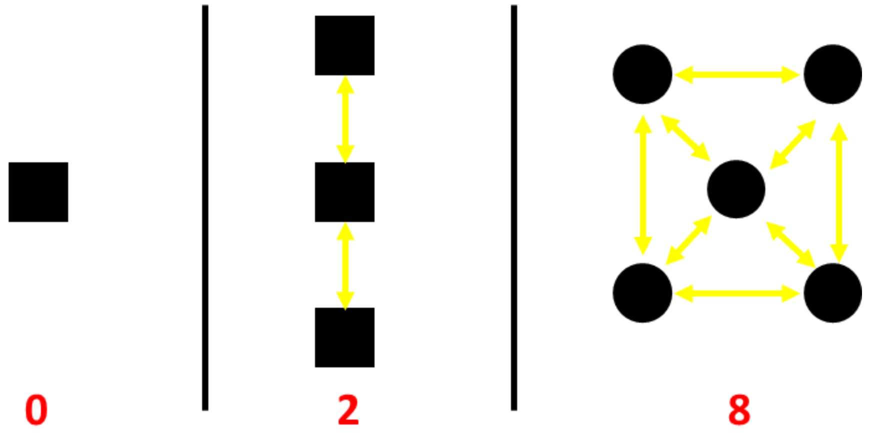


Figure 4.9.1. The visual stimuli used in the translating conditions in experiment 2 and 3, where the central element for those with multiple stimuli present is fixated on by the participant as in experiments 2 and 3. This will create the changes in interobject distance relative to the central element. Left: the *single translating square* has 0 visual separations because it is a solitary object; Middle: The *triplet translating* squares have 2 visual separations between the central square and flanking squares because they are stacked in a line and Right: the *translating_5* dots that due to their 2-1-2 formation have 8 visual separations between the objects.

4.8.3. Post-hoc observation

A post-hoc observation made on the percentage signal change in each condition for the left and right hemisphere ROIs suggests that the right hemisphere has a stronger selectivity for visual separation (interobject distance and visual angle) than the left hemisphere. This finding supports the general view that the right parietal lobe is more concerned with spatial processing than the left (Husain & Nachev, 2006). Neuropsychological evidence regarding visual neglect has shown that damage to the right hemisphere produces left sided neglect (Vallar & Perani, 1986). This neglect includes ignoring objects or people to the left-hand side or being unable to draw the left part of a person or object due to contralateral damage (Driver & Mattingley, 1998; Halligan, Fink, Marshall, & Vallar, 2003).

4.8.4. Conclusion

Experiment 3 used complex stimuli to explore interobject distance and visual angle, components of visual separation, and its effects on SPL function. Results suggested that in more complex visual stimuli, relative changes in ratios of visual angle or interobject distances are important for the function of the SPL. However, the higher numerosity of visual separations could play a role in increasing the tendency towards activation for stimuli where there are no changes in visual separation.

Chapter 5 – SPL Parcellation

5.1 Secondary anatomical question

In chapter 1 we referred to a paper by Wang et al., (2015) who parcellated the SPL into five distinct areas using a range of anatomical and functional criteria. We move on now to seeing where the results from the three experiments reported in this thesis fall within their SPL parcellation, as well as returning to the eleven studies discussed in chapter 1 to see where their activation lies in relation to Wang et al., (2015) parcellation, and whether their activations lie within one region or are spread across the SPL.

This secondary anatomical question produced a number of additional questions that were introduced in chapter 1. Using the DTI SPL parcellation maps provided to us by Dr Wang, we will first overlay the results from conditions 3 and 5 from experiment 1 to see where they lie within the five distinct subregions of the SPL. These two conditions constituted a replication of the Vandenberghe et al., (2001) study which Wang et al., (2015) also identified as being in a specific area of the SPL that they termed SPL5. It will be interesting to determine if our activation for conditions 3 and 5 were also present in SPL5, or in another of the distinct subregions identified by Wang et al., (2015). The teleporting condition of experiment 2 followed some of the constraints of the Vandenberghe et al., (2001) study such as the ten pre-determined locations and the frequency of left, right and crossing the midline shifts, however, there was no fixed static element (fixation cross). Would the absence of a fixed element change the activation location relative to Wang et al.'s, (2015) SPL parcellation? The absence of the fixed element removed the change in visual separation that was evident in conditions 3 and 5 and in Vandenberghe et al., (2001). However, in experiment 2, where there was no change in visual separation as in the triplet conditions, adaptation occurred when the triplets smoothly translated. When the triplet appeared to ‘jump/teleport’ to its next location, adaptation failed resulting in an expectation that the same sub-regions(s) of the SPL being involved because we proposed that visual separation recalculated at each new location in the *triplet teleporting* condition. In experiment 3, which explored visual separation split into two components: interobject distance and visual angles. The conditions *translating_5*, *CD4UpDown*, *CD4Rotate* will be overlayed on to the DTI maps to determine if the activation observed in each of these conditions fall into a specific SPL subregion.

In addition to the results of this thesis, the eleven studies with selective SPL activation reviewed in chapter 1 will also be plotted on to the SPL DTI maps to determine if they fall within one distinct area or a number of them, or outside Wang’s regions. Finally, each of the five subregions that were initially identified using anatomical criteria were attributed to functional specialisations which Wang et al., (2015) allocated based on previous papers. The results from experiments 1, 2 and 3 will be compared to the functional specialisations that Wang et al., (2015) identified for each of the subregions. This comparison will evaluate Wang et al's., (2015) functional statements against our own conclusions for the results we observed in experiments 1, 2 and 3 to see if there are any commonalities.

5.2 Wang et al., (2015) paper – key points

In chapter 1 we introduced a secondary anatomical question relating to the study by Wang et al., (2015) who used a variety of neuroimaging techniques to identify five distinct areas of the SPL and also provided suggested functions for each subregion (see Figure 5.2.1). The neuroimaging techniques that Wang et al., (2015) used comprised of structural, resting-state functional connectivity and coactivation patterns in published literature to determine the five subregions and their specific functionality. The structural connectivity parcellation calculated a maximum probability map for each voxel and its most probable location within MNI space, using diffusion probabilistic tractography and cross-correlation matrices, where the probability maps were then transformed to the Colin27 template within MNI space (Wang et al., 2015). The resting-state preprocessing steps created a four-dimensional time series for each of their twenty participants in MNI standard space. Coactivation patterns derived from approximately 7500 PET and fMRI neuroimaging studies from the BrainMap database (Laird, Eickhoff, Fox, Uecker, Ray, Saenz et al., 2011; Laird, Eickhoff, Kurth, Fox, Uecker, Turner et al., 2009) were used to determine coactivation connectivity patterns within the whole brain and the seed map voxels. Each voxel (SPL cluster and other brain voxels) had a connectivity probability calculated and then they were transformed into MNI space and a mean probability map was calculated for each of the five subregions identified in the SPL. The combination of the considerable number of steps required to identify the five distinct areas within the SPL allowed Wang et al., (2015) to expand upon previous parcellations of this brain region, which had included cytoarchitectonic properties (Scheperjans, Hermann, Eickhoff, Amunts, Schleicher, & Zilles, 2008) and anatomical connectivity patterns that also found five SPL subregions (however only one was within Wang’s SPL5 subregion at coordinates x19, y-63, z53 from Mars, Jbabdi, Sallet, O'Reilly, Croxzon, Olivier et al., (2011), by investigating the relationship between structural, resting-state functional connectivity and coactivation patterns to determine parcellation of the SPL. This combination of neuroimaging techniques provided a robust parcellation process involving more parameters than previous parcellations and why it is being used for this thesis. Wang et al., (2015) then investigated the connectivity patterns of the five identified regions to the whole brain before determining subregion functionality.

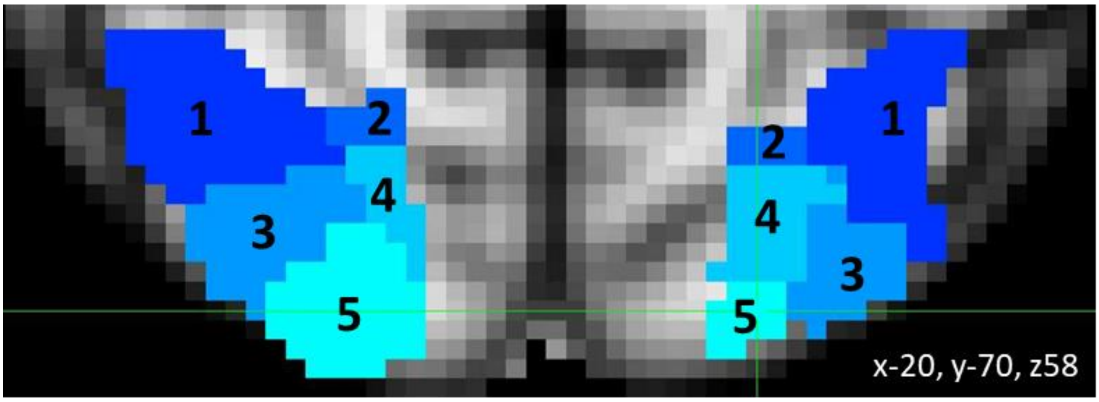


Figure 5.2.1. The five subregions shown bilaterally as proposed by Wang et al., (2015) represented in shades of blue and numbered. The coordinates for this slice are x-20, y-70, z58

The five distinct subregions of the SPL were bilateral across the two hemispheres. Moving on from the anatomical structural subregions, the functional subdivisions of each of the five areas of the SPL will provide interesting information relating to the processing of visual information. To determine the functionality of the different subregions, Wang et al., (2015) performed behavioural domain and paradigm class analyses and used forward and reverse inference to determine function specificity. They discovered different functions associated with each subregion in the left and right hemispheres (see Table 5.2.2). They found that action processes were predominantly found in the two anterior subregions whereas the remaining three posterior subregions were predominantly found to be involved with visual perception and spatial cognition (Wang et al., 2015).

Table 5.2.2. The functional characteristics identified by Wang et al., (2015) and which are associated with each SPL subregion.

SPL Subregions	vision motion	observation	space	execution	imagination	vision shape	language orthography	sexuality	working memory	reasoning	motor learning	attention
L1	✓	✓	✓	✓	✓							
R1	✓	✓	✓	✓		✓	✓	✓	✓			
L2				✓								
R2				✓							✓	
L3			✓			✓				✓		
R3	✓		✓	✓		✓						
L4	✓		✓	✓		✓			✓	✓		✓
R4	✓	✓	✓	✓	✓	✓			✓			
L5	✓		✓			✓			✓			✓
R5			✓	✓		✓			✓		✓	✓

It will be interesting to determine whether the results from the three experiments performed in this thesis lie within a specific subregion of Wang et al.'s, (2015) parcellated SPL. This will in turn provide an insight into the functionality of that subregion and whether our findings are consistent with Wang's attributions of functionality to subregions. The ROI masks that were also created to focus the experimental analyses will also be overlaid upon the SPL parcellation to determine where they sit within the five subregions. Finally, we can revisit the studies reviewed in chapter 1 to see where the peak SPL activation they reported lies in relation to the SPL parcellation and were they are consistent with our experimental results.

5.3 Method

The Wang et al., (2015) study used different neuroimaging methods to determine the five subregions of the SPL. They created probability maps from structural, resting-state, and coactivation parcellation to reach a consensus map containing the voxels that overlapped across the different parcellation maps, but this also included unallocated voxels between the subregions where there was no overlap. The unallocated voxels would make our questions harder to address. For this reason and after taking advice from the research group of Wang et al., (2015) study we used the DTI parcellation, which they sent us a nifti file of. This contained no gaps or unallocated voxels between the subregions and was used as the parcellation map on which we overlaid our ROIs and experimental results.

The DTI parcellation map was initially overlaid on top of a 2mm MNI template brain in standard space using FslView (part of the FRMIB software Library). It is important to note that experiment 1 was completed prior to a scanner upgrade at CINN, whereas experiments 2 and 3 were completed using the same participants and within the same scanner run, after the scanner upgrade took place. For this reason, experiment 1's ROI and results are reported separately from experiments 2 and 3. The ROIs were overlaid on top of the DTI parcellation map and the transparency for the individual ROIs was reduced to 30% so that those voxels that appeared in multiple ROIs would appear darker. Each of the contrasts used for the ROI masks (*road – flow* and *EML* vs *baseline*) used individual thresholds for every participant and the experimental conditions reported in this chapter had a voxelwise threshold of z=3, with a cluster p threshold of <0.05.

Each of the key conditions group results were then overlaid on top of the DTI parcellation map and relevant ROIs, using the thresholded z-stat image, and examined individually to determine which activation appears within the anatomical subregions of the SPL as identified by Wang et al., (2015). Functional specificity is then investigated to determine if those functions characterized by Wang and colleagues are consistent with the findings and conclusions of our results.

Finally, the peak coordinates, including sub-peaks, from each of the studies in chapter 1 were identified using the cross hairs of the FslView images, to determine whether they sit within a specific SPL subregion. Each set of coordinates will be looked at individually. Functional specificity will also be examined to see if they are consistent with both Wang et al., (2015) characterization and our findings.

5.4 Results: overlaying whole-brain contrast results onto the Wang parcellation

5.4.1. ROI for Experiment 1 and Experiments 2 and 3

In Figure 5.4.1. the ROI for experiment 1 appears superior to the DTI parcellation around coordinates x-20, y-60, z54, however the ROI appears at the top of the DTI parcellation map in SPL2, SPL3 and SPL4 bilaterally, around coordinates x-20, y-60, z62. In Figure 5.4.2. the ROI for experiments 2 and 3 also appears superior to the DTI parcellation around coordinates x-20, y-60, z54 although around the slice with the coordinates x-20, y-60, z60 the ROI appears to overlap SPL1, SPL2, SPL3 and SPL4 bilaterally.

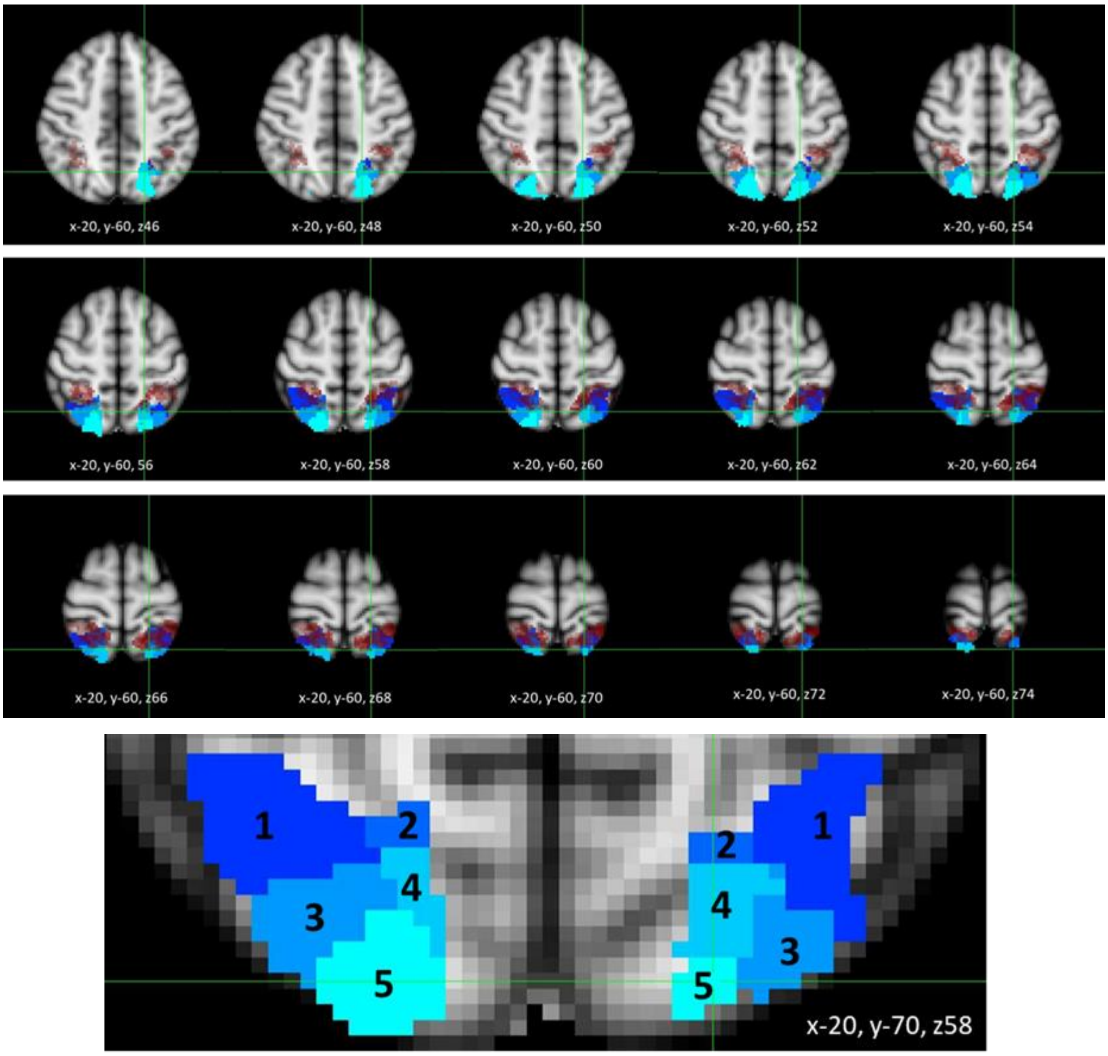


Figure 5.4.1. Varying coordinates of experiment 1 ROIs for each participant shown in red and Wang DTI parcellation shown in shades of blue. The darker the red voxels are ones where the voxel was present in the ROI of a greater number of participants. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres.

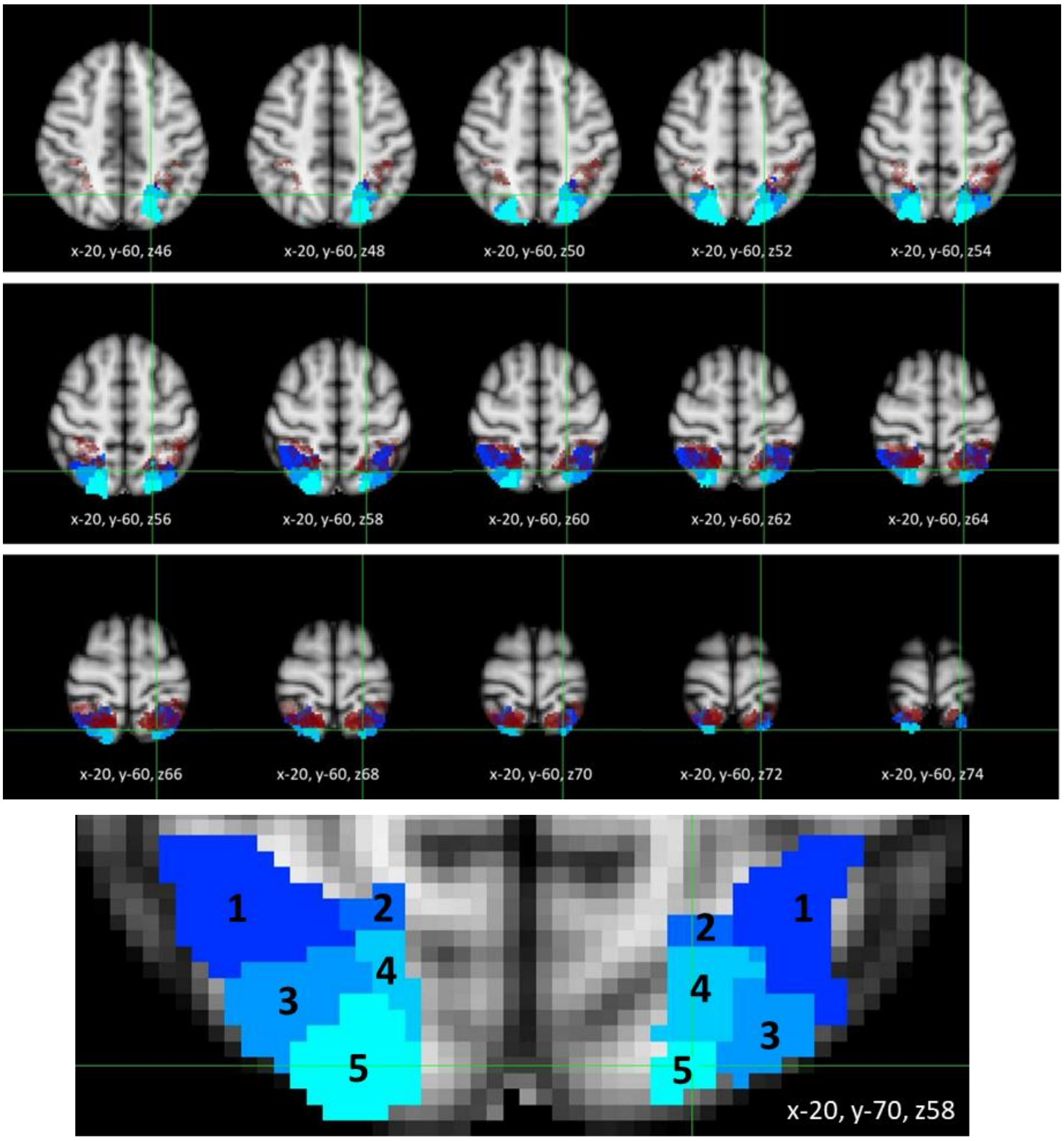


Figure 5.4.2. Varying coordinates of experiments 2 and 3 ROIs for each participant shown in red and Wang DTI parcellation shown in shades of blue. The darker the red voxels are ones where the voxel was present in the ROI of a greater number of participants. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres

5.4.2. Exp 1 – key conditions

The key conditions in experiment 1 for our current purposes were conditions 3 and 5, which were the Vandenberghe et al., (2001) replications. Figure 5.4.3. shows the group activation from condition 3 overlaid on top of the ROIs for experiment 1 and the SPL DTI parcellation from Wang et al., (2015). Activation occurs primarily in the left hemisphere and initially superior to the SPL parcellation (see slice x-20, y-60, z54) before overlapping subregions SPL1, SPL2 and SPL4. Activation in the right hemisphere were in SPL4 (see slice x20, -60, 68).

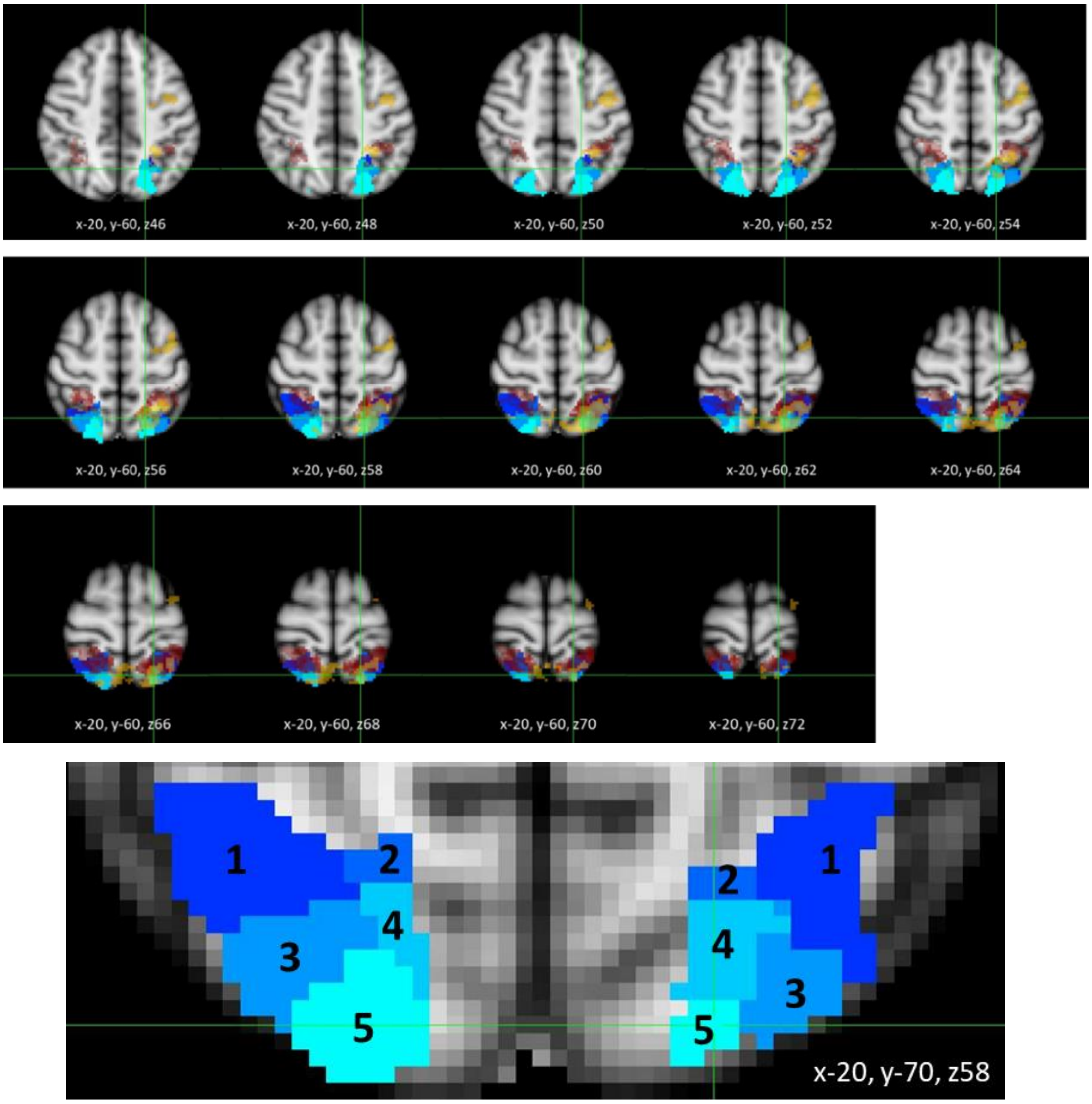


Figure 5.4.3. Slices showing condition 3 in orange, Experiment 1 ROI masks in red and the Wang DTI parcellation in shades of blue. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres

Condition 5 of experiment 1 again shows activation superior to the Wang et al., (2015) parcellation (see Figure 5.4.4. slice x-20, y-60, z50). There was a more diverse spread of activation bilaterally where activation overlaps SPL1, SPL3, SPL4 and SPL5 (see Figure 5.4.4. slice x-20, y-60, z58) in the right hemisphere and across all SPL subregions in the left hemisphere.

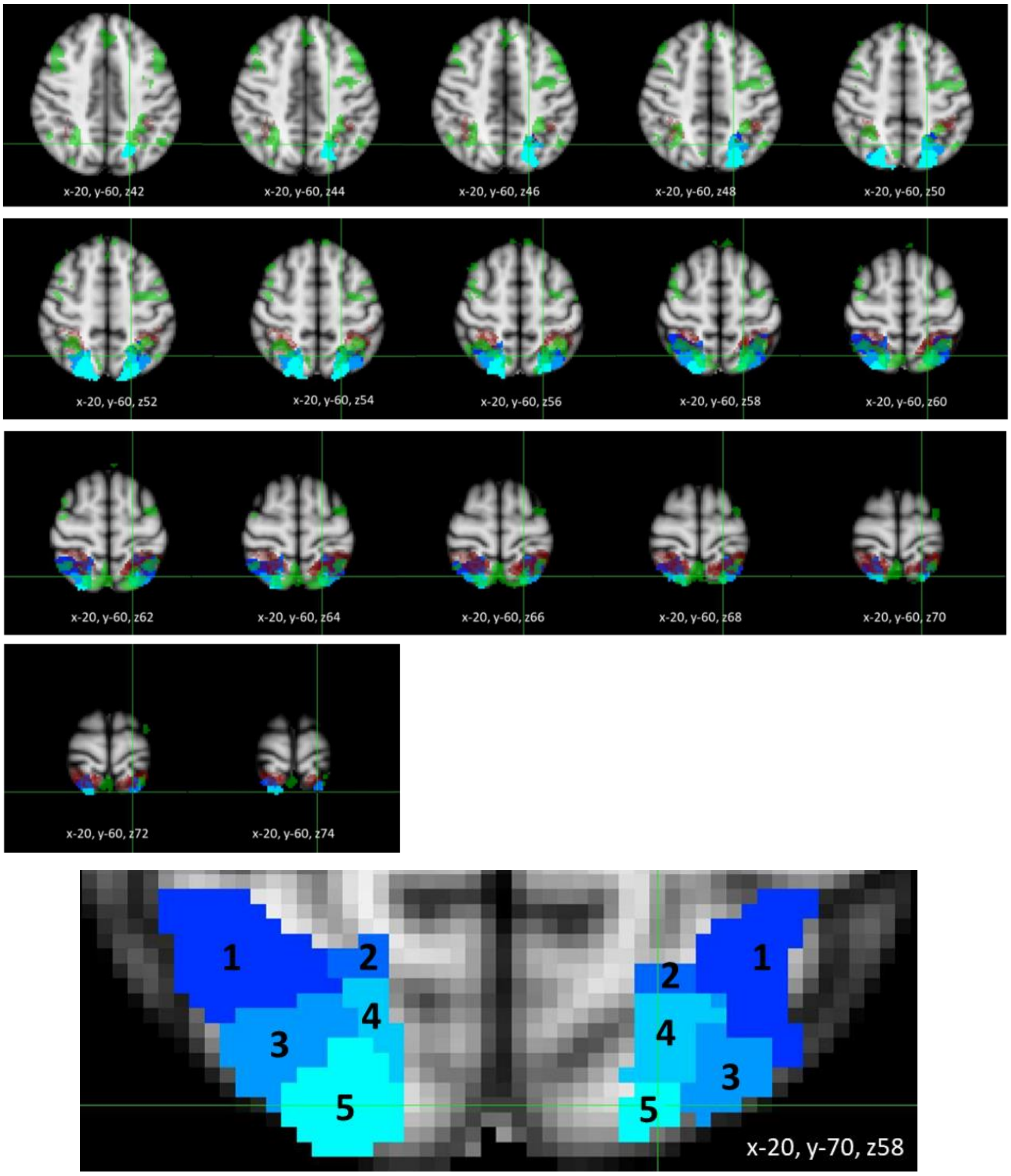


Figure 5.4.4. Slices showing condition 5 in green, Experiment 1 ROI mask in red and Wang DTI parcellation in shades of blue. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres.

Following Vandenberghe's analysis, we computed a conjunction mask of the overlapping voxels of conditions 3 and 5 that shows activation in the left hemisphere, and spread across SPL subregions SPL1, SPL2 and SPL4 (see Figure 5.4.5. slice x-20, y-60, z58). There are two distinct areas of activation observed with one solely within SPL1 and the other spans SPL2 and SPL4 (see Figure 5.4.5. slice x-20, y-60, z62). The two individual components of the conjunction mask had a voxelwise threshold of z=3, with a cluster p threshold <0.05. There is a reduction in the number of SPL subregions that are activated in the conjunction analysis (SPL1, SPL2 and SPL4) compared with the activation in conditions 3 and 5 combined (all five SPL subregions) due to the conjunction showing the overlap of the two conditions. The conjunction analysis activated the same subregions as condition 3 when viewed separately from condition 5 in the left hemisphere but condition 3 had additional activation in SPL4 in the right hemisphere that was not present in the conjunction analysis.

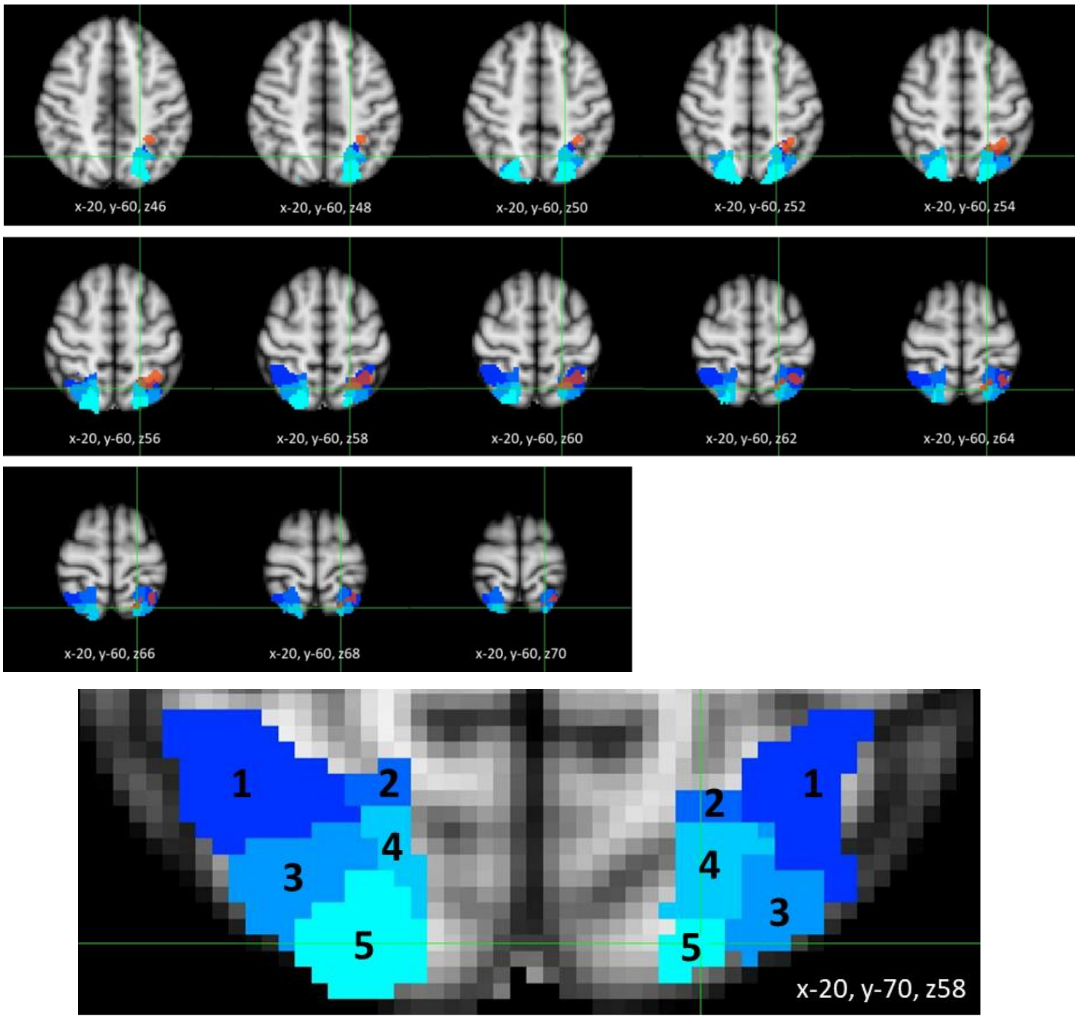


Figure 5.4.5. Conjunction mask consisting of overlapping voxels in both conditions 3 and 5, voxels in red and Wang DTI parcellation in shades of blue. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres.

5.4.3. Exp 2 – key condition

In experiment 2, the *triplet teleporting* condition produced high activation bilaterally. With activation initially superior to the SPL DTI parcellation as well as overlapping SPL4 in the left hemisphere (see Figure 5.4.6. slice x-20, y-60, z52) and SPL5 in the right hemisphere. At coordinates x-20, y-60, z56 activation is observed in all subregions in both the left and right hemispheres (see Figure 5.4.6.). This condition followed many of the same constraints as Vandenberghe et al., (2001) study but the main difference being that the three squares moved in unison which we predicted would not activate the SPL. The *triplet teleporting* condition is believed to have broken adaptation resulting in the SPL treating each new location as novel and recalculating visual separation. It is therefore not surprising that this condition has activated the same areas of the Wang et al., (2015) parcellation as conditions 3 and 5 of experiment 1, or the peak coordinates reported by Vandenberghe et al., (2001). Furthermore, when the conjunction analysis from experiment 1 (conditions 3 and 5) were laid over the *triplet teleporting* condition there was some overlap of active voxels that spanned SPL1, SPL2 and SPL4 of Wang's SPL subregions in the left hemisphere (see Figure 5.4.7.). These overlapping active voxels are consistent with our suggestion that the teleporting triplet condition breaks adaptation that occurs when the same visual stimuli smoothly translated, and therefore activate the same neurons as conditions 3 and 5. However, note, that there was a scanner upgrade and a change of participants between experiment 1 and experiments 2 and 3 which could have reduced the overlap between the conjunction analysis voxels and the *triplet teleporting* condition.

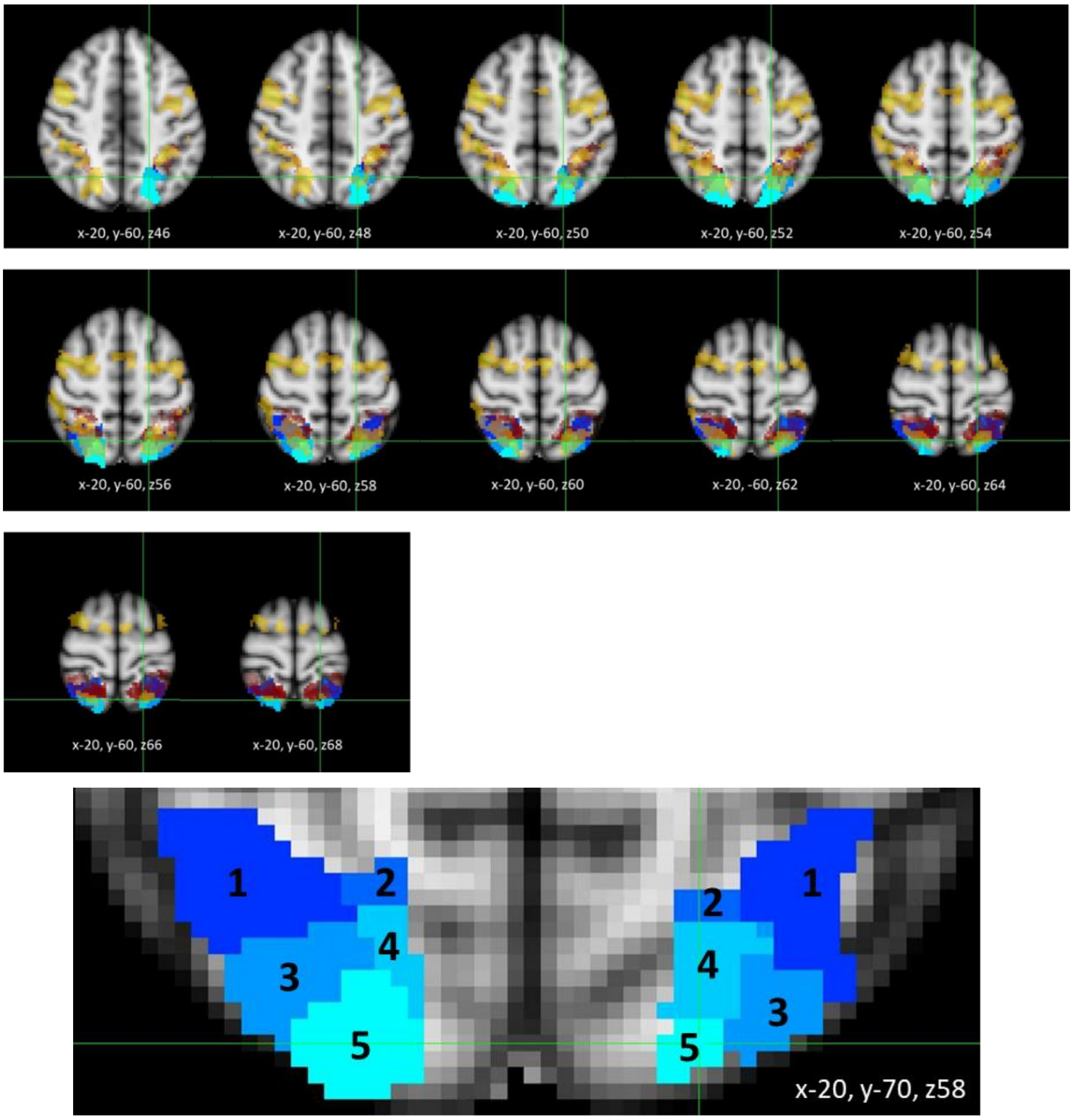


Figure 5.4.6. Slices showing *triplet teleporting* in orange, Experiment 2/3 ROI mask in red and Wang DTI parcellation in blue. Bottom panel shows numbered Wang et al., (2015) SPL parcellation for both hemispheres.

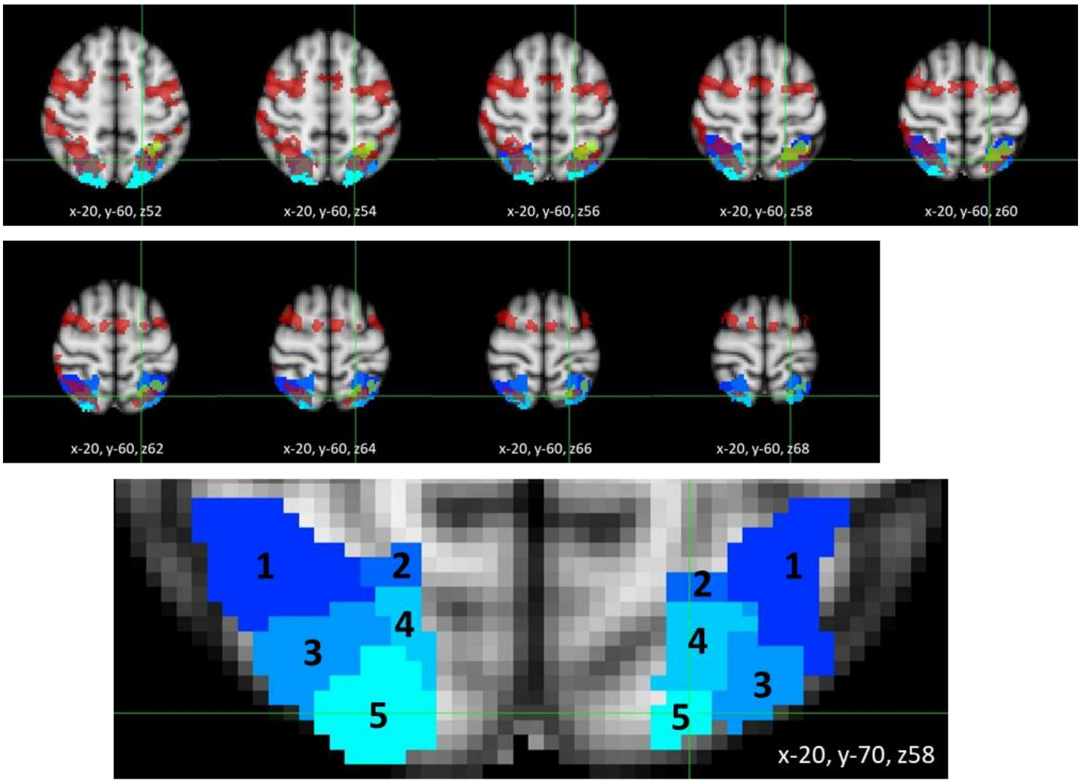


Figure 5.4.7. Wang et al., (2015) SPL parcellation in numbered shades of blue. Triplet teleporting condition in red which turns purple for voxels overlapping SPL parcellation. Conjunction analysis mask of conditions 3 and 5 is in green.

5.4.4. Exp 3 – key conditions

In experiment 3 the conditions were created to explore visual separation by breaking it down into two components: interobject distance and visual angle. The *translating_5* condition was included to determine if more complex visual stimuli that smoothly translates across the screen would follow the results of the previous translating conditions of experiment 2 that consisted of a single square and triplet squares. Activation in the SPL was therefore not expected but it occurred in SPL1 and SPL4 (see Figure 5.4.8. slice x-20, y-60, z56) in the left hemisphere, continuing to SPL1, SPL2, SPL3 and SPL4 (see Figure 5.4.8. slice x-20, y-60, z60) in the right hemisphere.

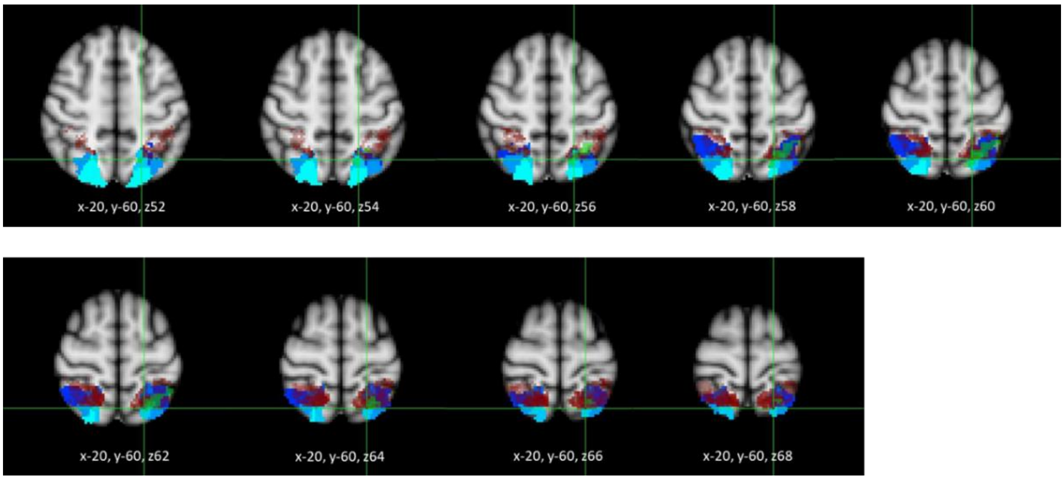


Figure 5.4.8. Slices showing *translating_5* in green, Experiment 1 ROI mask in red and Wang DTI parcellation in blue.

The *CD4UpDown* condition was a strong activator in the SPL which we believe is due to the simultaneous change in both interobject distance and visual angle. Activation occurred bilaterally across subregions SPL1 and SPL4 (see Figure 5.4.9. slice x-20, y-60, z52) in the left hemisphere and at the edges of subregions SPL3, SPL4 and SPL5 in the right hemisphere. This progressed to subregions SPL1, SPL2, SPL3 and SPL4 (see Figure 5.4.9. slice x-20, y-60, z62) in the right hemisphere and across all subregions in the left hemisphere.

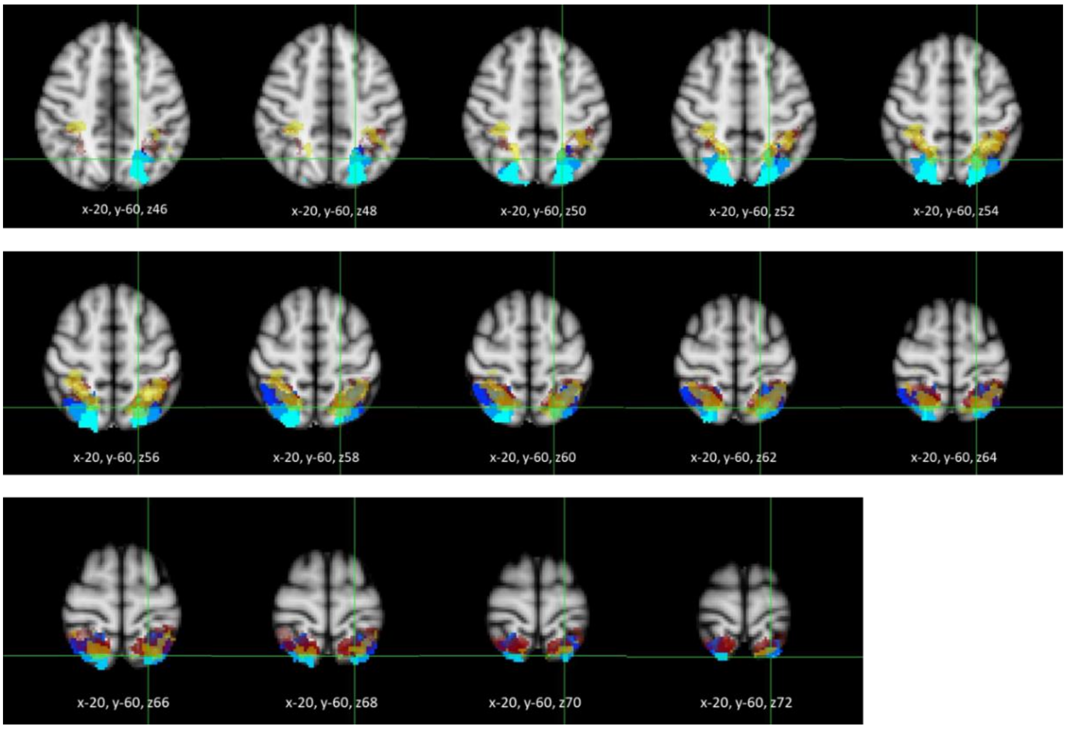


Figure 5.4.9. Slices showing *CD4UpDown* in orange, Experiment 1 ROI mask in red and Wang DTI parcellation in blue.

The *CD4Rotate* condition had changes to visual angle only and produced activation in the left hemisphere only across subregions SPL1, SPL2, SPL3 and SPL4 (see Figure 5.4.10. slice x-20, y-60, z64).

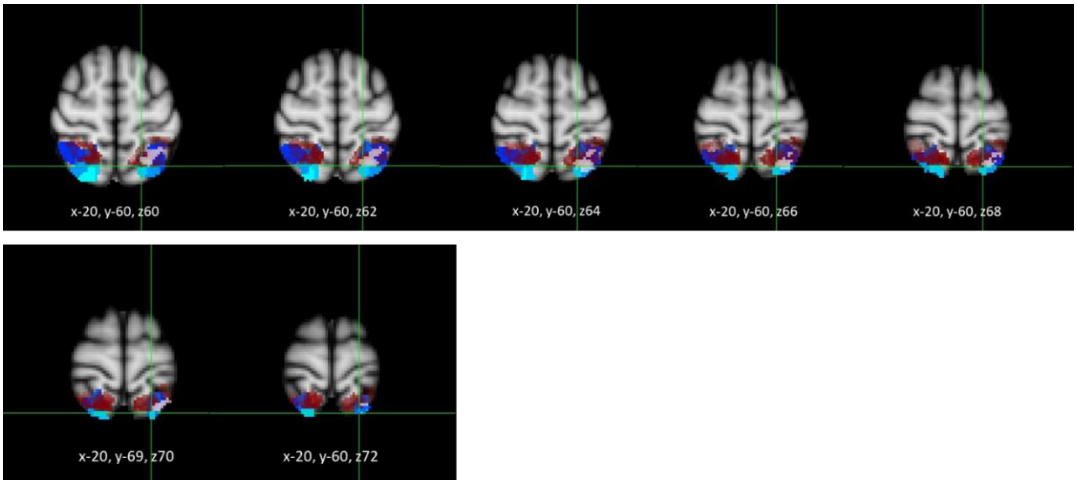


Figure 5.4.10. Slices showing *CD4Rotate* in pink, Experiment 1 ROI mask in red and Wang DTI parcellation in blue.

5.4.5. Functional characteristics

Whilst the results of the key conditions of the three experiments in this thesis were spread across multiple subregions, there were some differences across hemispheres in some conditions. This produced a number of functional characteristics that were featured more often: execution, space, vision shape and vision motion (see Figure 5.4.11.)

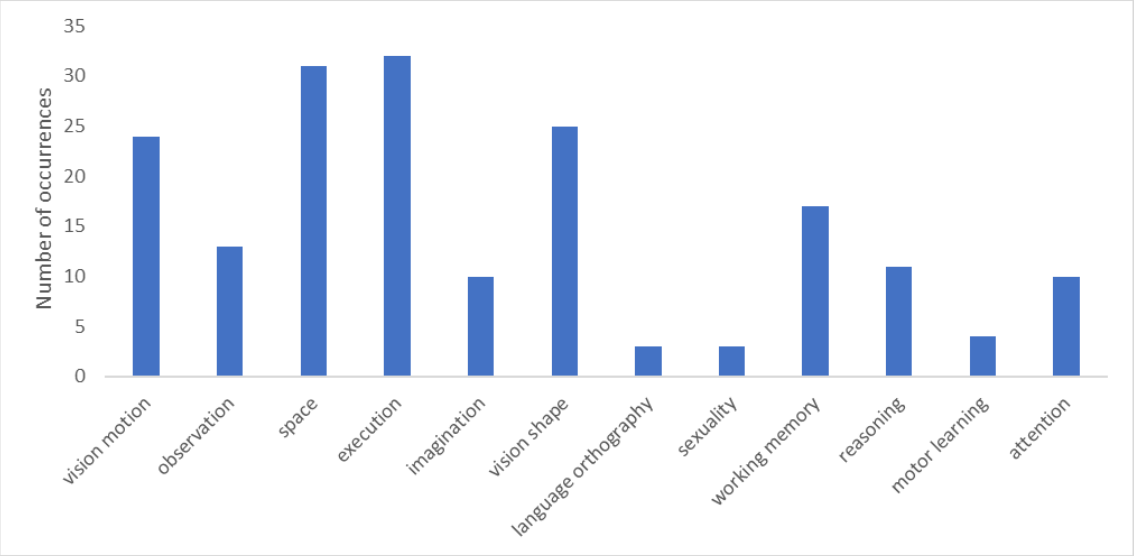


Figure 5.4.11. Number of occurrences of functional characteristics listed by Wang et al., (2015) summed across all sub-regions and both hemispheres

Referring back to Table 5.2.2. which listed the functional specificity for each SPL subregion per hemisphere as suggested by Wang et al., (2015): for conditions 3 and 5, which followed Vandenberghe et al., (2001) constraints and had activation in SPL1, SPL2 and SPL4 primarily in the left hemisphere for condition 3 (covert viewing of a displacing square). The functional characteristics suggested by Wang et al., (2015) are as follows: vision motion, observation, space, execution, reasoning and attention. For condition 5 (overt viewing of displacing square), activation was observed in SPL1, SPL3, SPL4 and SPL5 in the right hemisphere and all SPL subregions in the left hemisphere which brings additional functional characteristics to those listed for condition 3: language orthography, and sexuality which were specific to SPL1 in the right hemisphere. Condition 5 especially produced activation that spread across multiple SPL subregions: SPL5 (right hemisphere), SPL4 (left hemisphere), SPL3 (right hemisphere) and SPL1 (left hemisphere) which gives similar functional characteristics: vision motion, space, vision shape, working memory, attention, execution, reasoning, observation, and imagination. The conjunction analysis mask of the overlapping voxels from conditions 3 and 5 focused the activation more narrowly within three subregions of SPL1, SPL2 and SPL4 in the left hemisphere that produced more limited functional characteristics: vision motion, observation, space, execution, imagination, vision shape, working memory, reasoning, and attention.

The *triplet teleporting* condition from experiment 2 was also a high activator and had activation across all SPL subregions bilaterally. It is therefore surprising that there is a similar array of activation across all subregions of the SPL as with conditions 3 and 5, and Vandenberghe et al., (2001) because of the 'jumping/teleporting' nature of displacement in that we suspect breaks adaptation, in the absence of a fixed element, which conditions 3, 5 and Vandenberghe et al., (2001) had but *triplet teleporting* did not.

The *translating_5* condition which had no changes in interobject distance or visual angle produced activation in the SPL1, SPL2, SPL3 and SPL4 subregions in the left hemisphere which are linked with the following functional characteristics suggested by Wang et al., (2015): vision motion, observation, space, execution, imagination, vision shape, reasoning, working memory, and attention. For the *CD4UpDown* condition which had changes to both interobject distance and visual angle, was a strong activator and covered multiple SPL subregions (SPL1, SPL2, SPL3, and SPL4) in the right hemisphere and across all subregions in the left hemisphere. The list of functional characteristics included all the characteristics combined for conditions 3 and 5. For condition *CD4Rotate* there was activation in the left hemisphere only and across SPL subregions SPL1, SPL2, SPL3, and SPL4 which makes the list of functional characteristics as follows: vision motion, observation, space, execution, imagination, vision shape, reasoning, working memory, and attention.

5.5 Other studies from chapter 1

Eleven studies were reviewed in chapter 1 because they reported selective activation within the SPL and whilst the conclusions for doing so were varied, we proposed a visual separation hypothesis that could explain much of the activation in the discussed studies. We now return to those studies and looking at each one individually to see whether the peak activation they reported also appeared in one of the SPL subregions suggested by Wang et al., (2015).

Conditions 3 and 5 of experiment 1 were replications of the Vandenberghe et al., (2001) study, which had SPL peak coordinates with activation in different SPL subregions (see Figure 5.5.1). Activation occurred in SPL1, SPL3, SPL4 and just outside SPL5 at Vandenberghe et al.'s, (2001) coordinates, which was replicated in condition 5, whereas condition 3 and the conjunction analysis mask focused the activation to SPL1, SPL2 and SPL4 subregions in the left hemisphere and in SPL4 for condition 3 in the right hemisphere. The Vandenberghe et al., (2001) coordinates show peak activation in the SPL for their conjunction analysis (overt and covert attention shifts) versus sustained attention and found peak activation at four different sets of coordinates (see Figure 5.5.1.). Our conjunction analysis had activation in the left hemisphere at coordinates x-24, y-57, z57 and x-33, y-54, z57, whereas Vandenberghe et al., (2001) had bilateral activation.(see Figure 5.5.2).

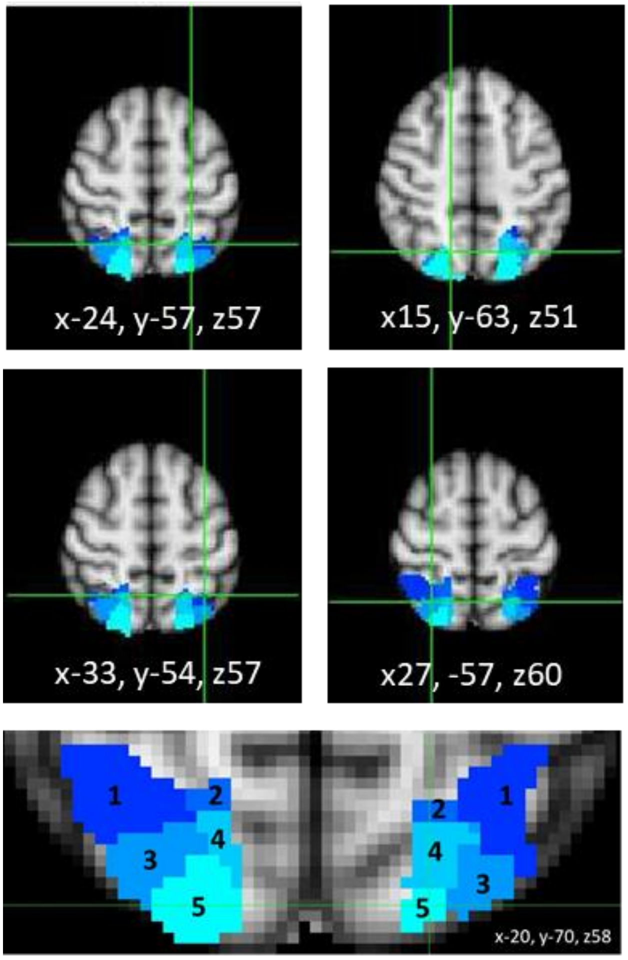


Figure 5.5.1. Wang et al., (2015) SPL DTI parcellation numbered and in blue shades. Vandenberghe et al., (2001) conjunction peak activations between covert and overt conditions. Top left: Crosshair at x24, y-57, z57 in SPL4; Top right: Crosshairs at x-15, y-63, z51 just outside SPL5; middle left: crosshairs at x33, y-54, z57 in SPL1; middle right: crosshairs at x27, y-57, z60 in SPL3.

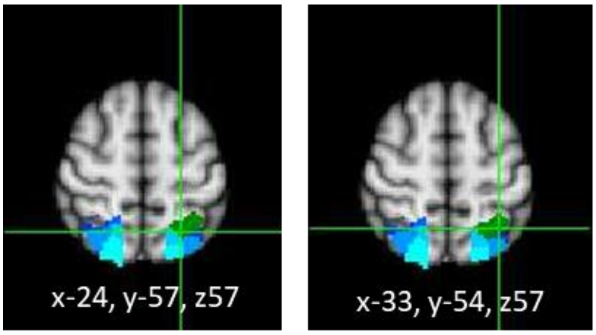


Figure 5.5.2. Wang SPL parcellation in shades of blue. Conjunction analysis of conditions 3 and 5 from experiment 1 in green. Crosshairs at the left hemisphere peak coordinates of Vandenberghe et al., (2001) peak activation of their conjunction analysis (overt and covert attentional shifts) and sustained attention.

The peak coordinates from Field et al., (2007) showed activation in subregions SPL1 (x35, y-48, z60) and SPL4 (x14, y-62, z60) in the left hemisphere, SPL4 (x-16, y-66, z58) and SPL5 (x-16, y-72, z52) in the right hemisphere. However, coordinates x-26, y-54, z56 in the left hemisphere were just outside the Wang parcellation, but near the SPL4 subregion (see Figure 5.5.3.).

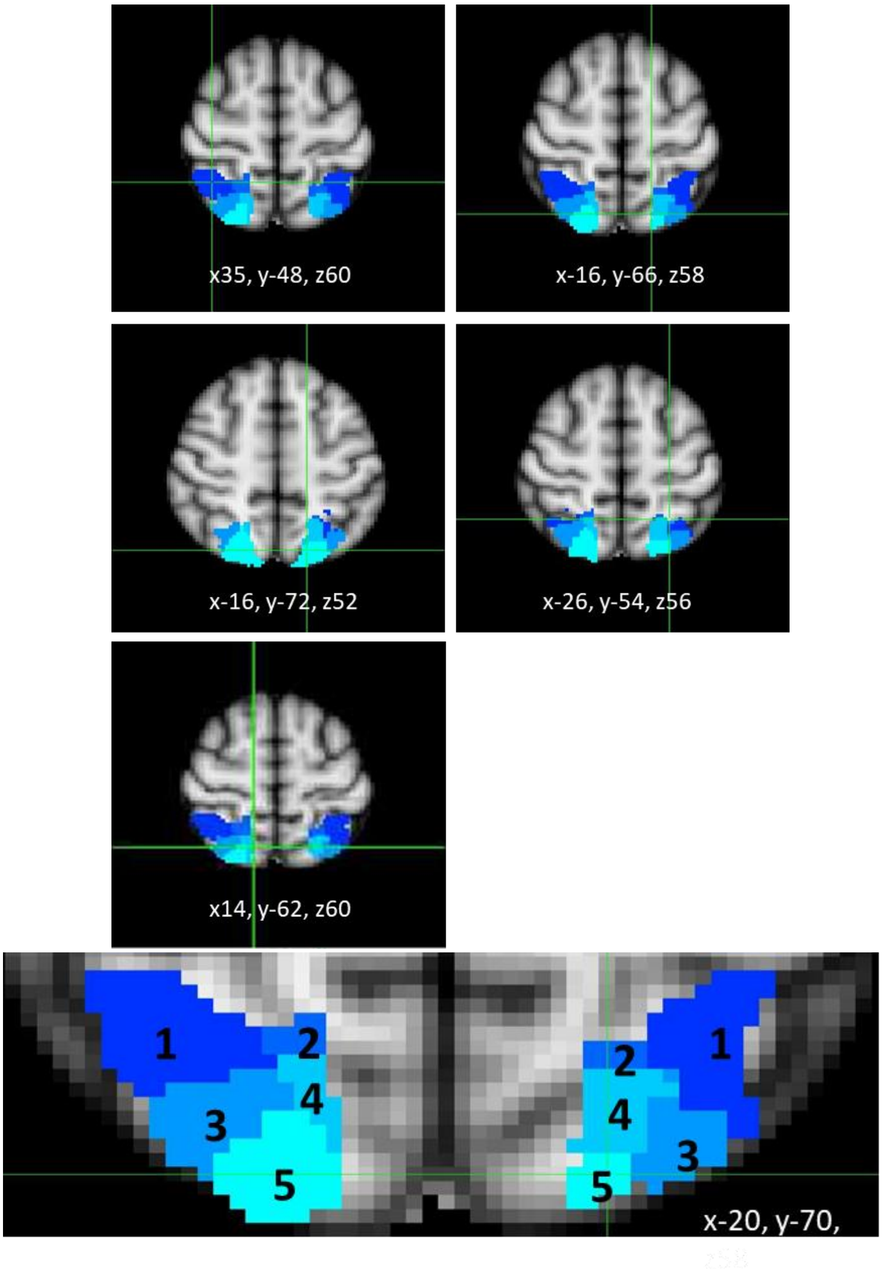


Figure 5.5.3. Peak cluster activations from Field et al., (2007) study where: the top left is in SPL1; top right is in SPL4; middle left is in SLP5; middle right just outside SPL4, third row is in SPL4. Bottom panel shows Wang parcellation with numbered subregions.

Ohlendorf et al., (2010) produced several peak coordinates which they reported were within the SPL region of the brain. Activation was shown in SPL1 (x24, y-54, z57) in the right hemisphere, (x-27, y-51, z51) in the left hemisphere; SPL4 (x-24, y-57, z54) in the left hemisphere and SPL3 (x21, y-57, z54) in the right hemisphere. The coordinates x21, y-60, z51 were just outside the SPL parcellation in the right hemisphere (see Figure 5.5.4.).

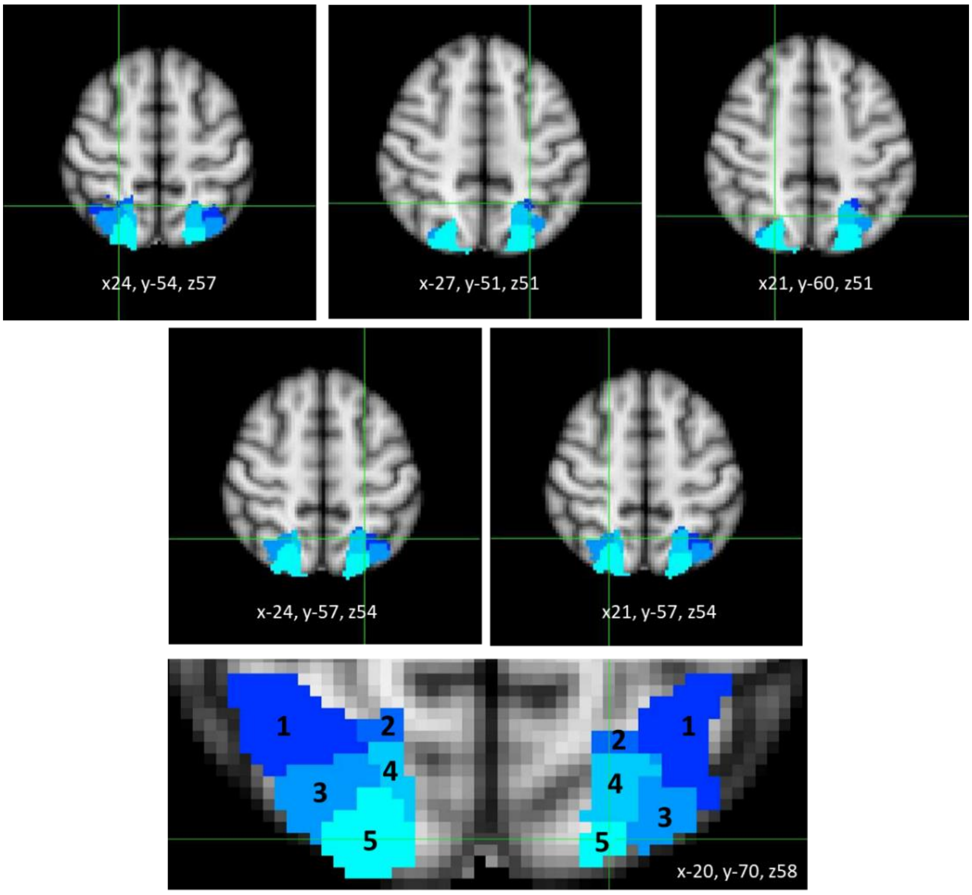


Figure 5.5.4. Peak cluster activations from Ohlendorf et al., (2010) study where: the top left is in SPL1; top middle is in SPL1; top right is just outside SPL parcellation; middle left is in SLP4; middle right is in SPL3. Bottom panel shows Wang parcellation with numbered subregions.

The peak coordinates reported for the Peuskens et al., (2001) optic flow study mostly appear in SPL4 although not all coordinates reported appeared within the SPL parcellation (see Figure 5.5.5.). Coordinates x-16, y-70, z60; x-22, y-60, z60; x18, y-69, z63; and x-21, y-63, z60 all appear in SPL4 in the left and right hemispheres, coordinates x24, y-60, y69 were in SPL3 in the right hemisphere, whereas x-12, y-57, z57 was just outside SPL4 in the left hemisphere. However, coordinates x-12, y-60, z66 did not appear in within the (Wang et al., 2015) SPL parcellation.

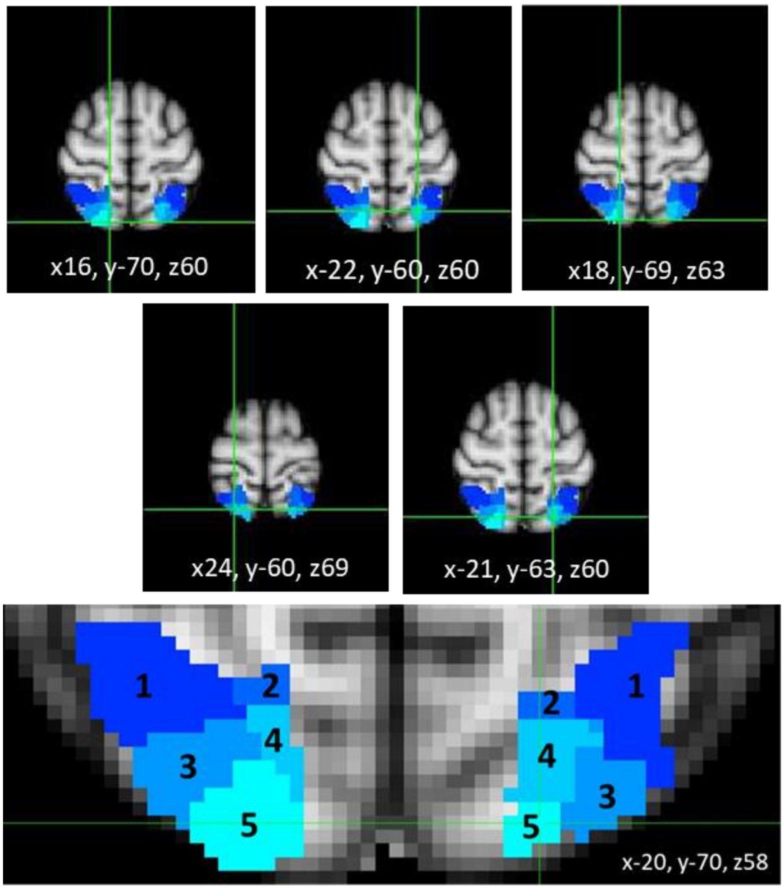


Figure 5.5.5. Peak cluster activations from Peuskens et al., (2001) study where: the top row all appears within SPL4; second row left is in SPL3, second row right is in SPL4 of Wang SPL parcellation. Bottom panel shows Wang parcellation with numbered subregions.

Also, for the Jordan et al., (2001) study there were some coordinates that did not fall within the SPL parcellation (x28, y-64, z48; x24, y-68, z48; x24, y-64, z48). There was activation in SPL3 at coordinates x-28, y-64, z48 in the left hemisphere and also activation in SPL3 in the right hemisphere (x24, y-56, z56) (see Figure 5.5.6.).

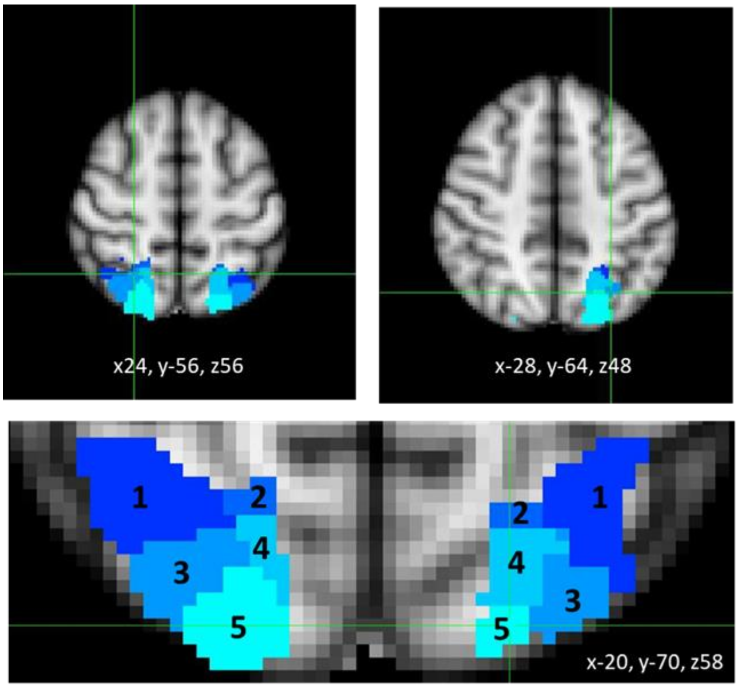


Figure 5.5.6. Peak cluster activations from Jordan et al., (2001) study where: the top left is in SPL3; top right is also in SPL3. Bottom panel shows Wang parcellation with numbered subregions.

Wolbers et al., 2008 study had one set of coordinates within the SPL1 subregion (x-24, y-54, z52) in the left hemisphere and one set of coordinates in SPL3 (x24, y-56, z56) in the right hemisphere. However, there were coordinates that did not appear within the SPL parcellation (x-30, y-60, 44; x32, y-60, z42) (see Figure 5.5.7). The Jovicich et al., (2001) study had one set of coordinates in SPL3 (x-27, y-57, z69) and another set of coordinates in SPL4 (x21, y-57, z72) appearing in the Wang et al., (2015) SPL parcellation (see Figure 5.5.8).

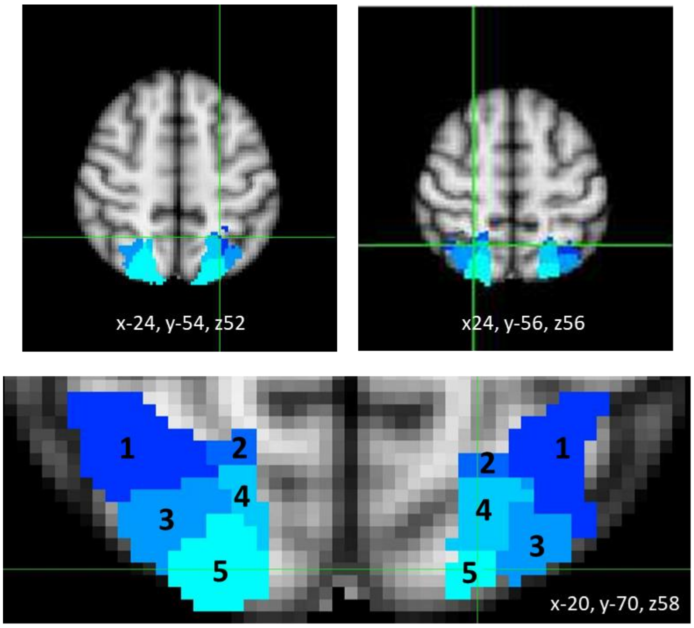


Figure 5.5.7. Peak cluster activation from Wolbers et al., (2008) study where: the top left is in SPL1 and top right is in SPL3. Bottom panel shows Wang parcellation with numbered subregions.

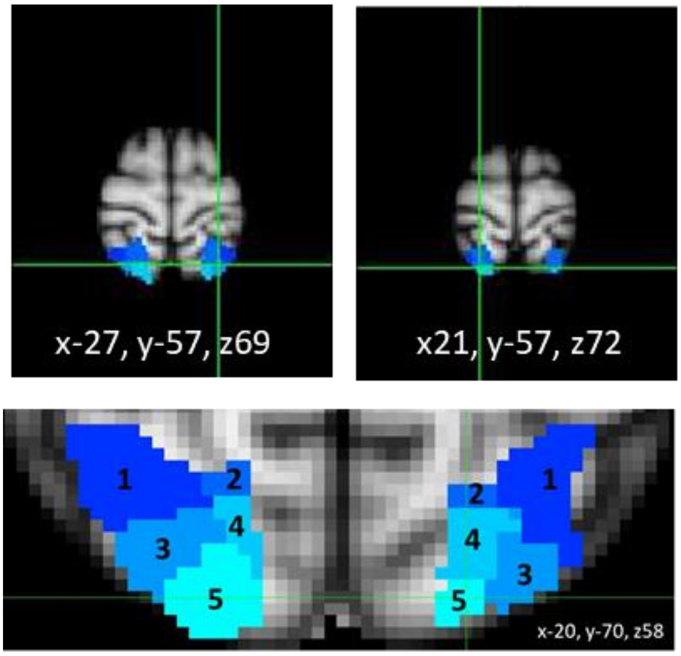


Figure 5.5.8. Peak cluster activation from (Jovicich et al., 2001) study where: the top left is in SPL3 and top right is in SPL4. Bottom panel shows Wang parcellation with numbered subregions.

The two peak coordinates reported by Billington et al., (2013) were found to be within the SPL parcellation. Coordinates x-21, y-68, z58 was in SPL5 and x-24, y-54, z62 was in SPL2, both in the left hemisphere (see Figure 5.5.9.). In the Billington et al., (2010) study, peak activation was found within the SPL parcellation in SPL4 (x-20, y-59, z62) and SPL3 (x-28, y-61, z58) in the left hemisphere and in SPL5 (x20, y-67, z59) in the right hemisphere (see Figure 5.5.10.).

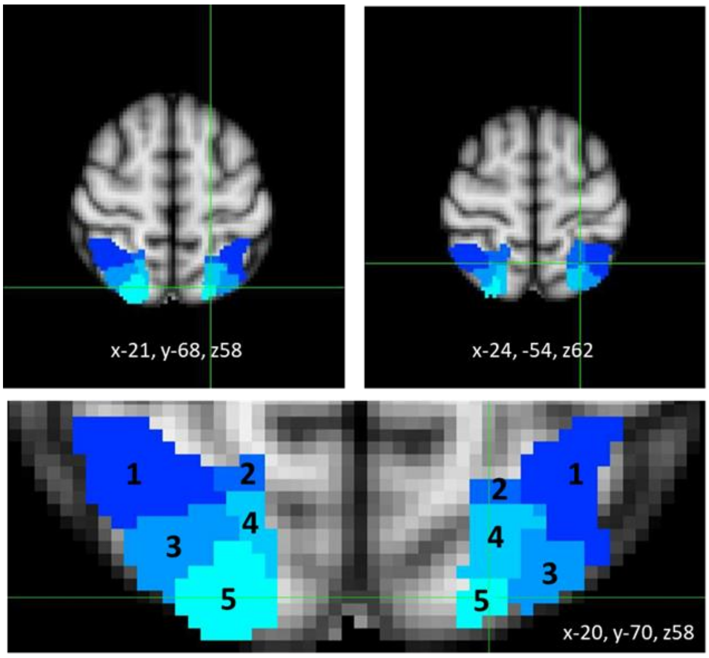


Figure 5.5.9. Peak cluster activations from Billington et al., (2013) study where: the top left is in SPL5; top right is also in SPL2. Bottom panel shows Wang parcellation with numbered subregions.

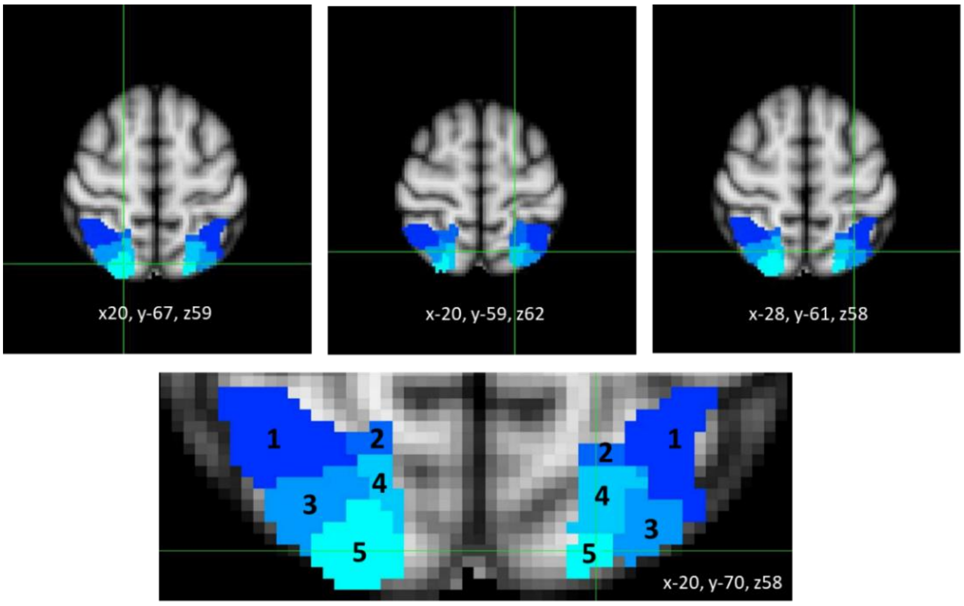


Figure 5.5.10. Peak cluster activations from Billington et al., (2010) study where the top left: is in SPL5, top middle: is in SPL4; top right: is in SPL3; bottom: Wang parcellation with numbered subregions.

In the Inman, (2014) study activation was also observed in SPL4 (x-18, y-66, z56) in the left hemisphere and in SPL3 (x26, y-62, z56) in the right hemisphere (see Figure 5.5.11.).

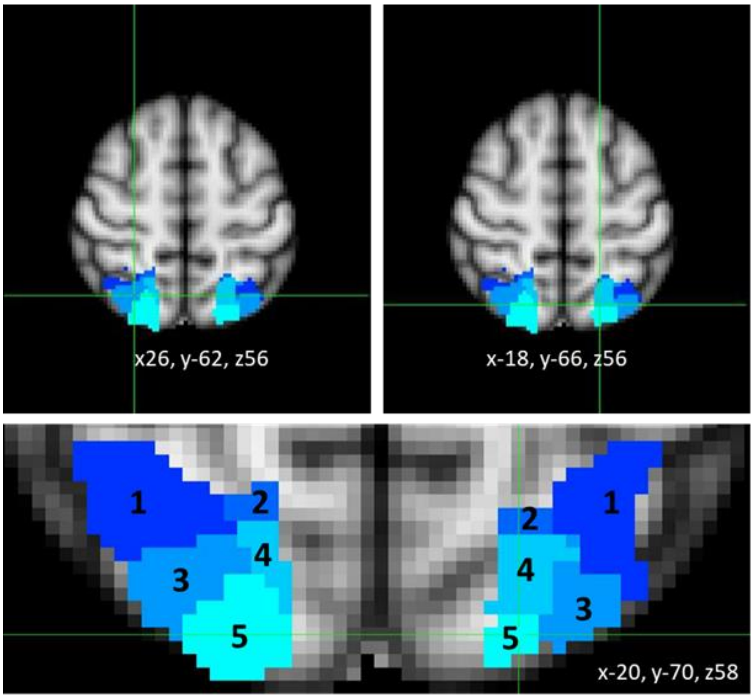


Figure 5.5.11. Peak cluster activations from Inman, (2014) study where: the top left is in SPL3; top right is in SPL4. Bottom panel shows Wang parcellation with numbered subregions.

The Wu et al., (2016) study used TMS at the coordinates that were within SPL5 subregion (x-20, y-70, z56) in the left hemisphere and (x20, y-71, z50) in the right hemisphere (see Figure 5.5.12.). This was the only study out of the eleven that used Wang et al., (2015) parcellation maps and specifically SPL5 as a focus of their research.

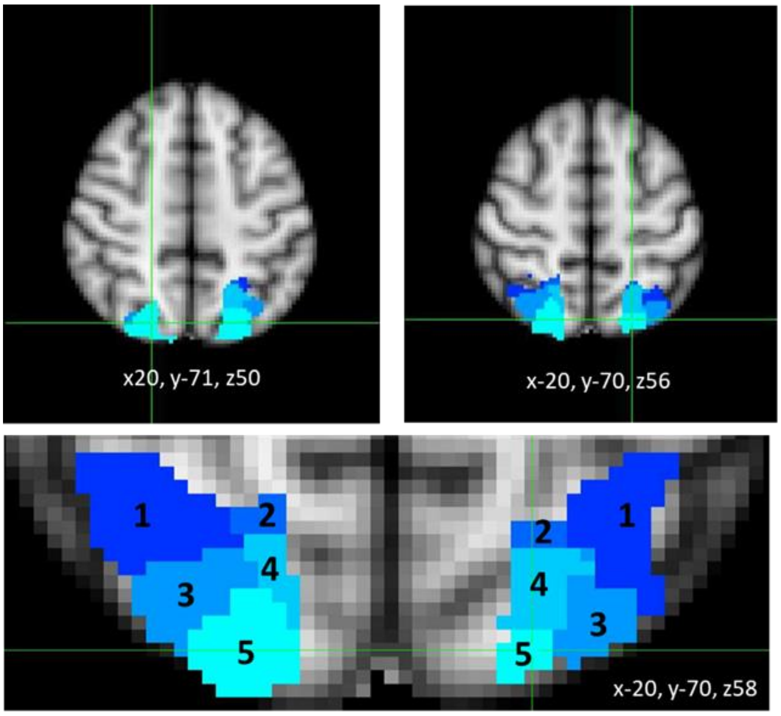


Figure 5.5.12. Coordinates used to direct TMS from Wu et al., (2016) study where: the top left is in SPL5; top right is also in SPL5. Bottom panel shows Wang parcellation with numbered subregions.

These studies produced peak activation in multiple SPL subregions as did our experimental data and in most of the studies the peak coordinates reported would lie in different SPL subregions to others from the same study. There were also several coordinates that did not fall into the SPL parcellation. In the left hemisphere the subregion that had the most peak coordinates was SPL4 followed by SPL1, SPL3 and

SPL5, whereas in the right hemisphere it is SPL3 and SPL4 (see Table 5.5.13.). When collapsing across hemispheres and conditions, the SPL subregion that had the most activation from our experimental data and the other studies combined was SPL3 (see Table 5.5.14.). Experiment 3 and the ROI masks (both Exp1 and Exp 2/3) did not activate SPL5, along with (Inman, 2014; Jordan, Heinze, et al., 2001; Jovicich et al., 2001; Ohlendorf et al., 2010; Peuskens et al., 2001; Wolbers et al., 2008), Vandenberghe et al., 2001a had activation just outside SPL5Billington et al., (2013) was the only study from those listed that had activations within the SPL2 subregion, although it consistently had activation in our experimental conditions.

Table 5.5.13. Peak coordinates with the Wang et al., (2015) SPL subregion that the coordinate is found in (if applicable), Harvard-Oxford Cortical Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) probability, Juelich SPL cytoarchitectonic areas 5M, 5L, 5Ci, 7A, 7M, 7P, 7PC (Scheperjans et al., 2008) probability, and group average z score for *Road – Flow* Localiser in both the left and right hemispheres. LOC (Lateral Occipital Cortex).

Author	Peak Coordinates	Wang SPL subregion	Probability of Harvard-Oxford	Juelich probability	Group Average Road - Flow Z scores
Billington et al., (2010)	-20, -59, 62	SPL4	24% SPL	79% 7A, 14% 7PC, 10% 7P, 9% 5L	3.81
	-28, -61, 58	SPL3	13% SPL	70% 7A, 9% 7PC, 7% 7P	0
	20, -67, 59	SPL5	56% LOC	70% 7P, 23% 7A	0
Billington et al., (2013)	-21, -68, 58	SPL5	68% LOC	59% 7A, 32% 7P	0
	-24, -54, 62	SPL2	50% SPL	57% 7A, 12% 7PC, 12% 5L,2% 7P	4.23
Field et al., (2007)	-16, -66, 58	SPL4	2% SPL, 58% LOC	61% 7A, 41% 7P	0
	-16, -72, 52	SPL5	58% LOC	38% 7P, 25% 7A,	0
	-26, -54, 56	Just outside SPL4	42% SPL	38% 7A, 31% 7PC, 10% 5L, 8% 7P,	3.36
	35, -48, 60	SPL1	57% SPL	42% 7PC, 13% 7A,	0
	14, -62, 60	SPL4	9% SPL, 47% LOC	64% 7A, 32% 7P 1% 5M	0
Inman (2014)	-18, -66, 56	SPL4	2% SPL, 53% LOC	72% 7A, 27% 7P	0
	26, -62, 56	SPL3	6% SPL, 58% LOC	62% 7A, 19% 7P, 8% 7PC	0
Jordan et al., (2001)	-28, -64, 48	SPL3	8 % SPL, 53% LOC	21% 7A	0
	28, -64, 48	None	1% SPL, 56% LOC	17% 7A, 10% 7P	0
	24, -68, 48	None	47% LOC	19% 7A, 12% 7P	3.19
	24, -56, 56	SPL3	24% SPL	61% 7A, 9% 7P, 2% 7PC, 1% 5L	3.28
	24, -64, 48	None	1% SPL, 51% LOC	13% 7P, 13% 7A	0
Jovicich et al., (2001)	-27, -57, 69	SPL3	26% SPL	65% 7A, 12% 7PC, 3% 5L	3.04
	21, -57, 72	SPL4	14% SPL	63% 7A, 38% 5L, 28% 7PC	0
Ohlendorf et al., (2010)	-27, -51, 51	SPL1	35% SPL	16% 7PC, 11% 7A, 9% 5L, 1% 7P	0
	-24, -57, 54	SPL4	29% SPL	39% 7A, 11% 7P, 9% 7PC, 4% 5L	3.6
	24, -54, 57	SPL1	40% SPL	48% 7A, 12% 5L, 9% 7PC, 1% 7P	3.57
	21, -60, 51	Just outside SPL	10% SPL	34% 7A, 6% 7P	0
	21, -57, 54	SPL3	17% SPL	58% 7A, 24% 7P, 5% 7PC	0
Peuskens et al., (2001)	-22, -60, 60	SPL4	23% SPL	75% 7A, 11% 7PC, 10% 7P, 2% 5L	3.95
	-21, -63, 60	SPL4	4% SPL, 56% LOC	83% 7A, 18% 7P	3.3
	-12, -60, 66	None	19% SPL	75% 7A, 16% 7P, 12% 5L, 3% 5M, 1%	0
	-12, -57, 57	None	21% SPL	58% 7A, 20% 7P, 13% 5L, 4% 5M, 3%	0
	16, -70, 60	SPL4	63% LOC	68% 7P, 12% 7A	0
	18, -69, 63	SPL4	14% SPL	66% 7P, 23% 7A	0
	24, -69, 69	SPL3	5% LOC	4% 7A, 1% 7P	0
Vandenberge et al., (2001)	-24, -57, 57	SPL4	29% SPL	46% 7A, 17% 7P, 14% 7PC, 8% 5L	3.82
	-33, -54, 57	SPL1	47% SPL	56% 7A, 35% 7PC	0
	15, -63, 51	just outside SPL5	1% SPL, 24% LOC	27% 7P, 10% 7A	0
	27, -57, 60	SPL3	17% SPL	80% 7A, 8% 7P, 7% 7PC, 2% 5L	0
Wolbers et al., (2008)	-24, -54, 52	SPL1	30% SPL	18% 7PC, 15% 7A, 11% 7P, 9% 5L	0
	-30, -60, 44	None	16% SPL	13% 7A	0
	24, -56, 56	SPL3	24% SPL	61% 7A, 9% 7P, 2% 7PC, 1% 5L	3.28
	32, -60, 42	None	7% SPL, 42% LOC	2% 7A	0
Wu et al., (2016)	-20, -70, 56	SPL5	63% LOC	61% 7A, 28% 7P	0
	20, -71, 50	SPL5	53% LOC	40% 7P, 18% 7A	0

Table 5.5.14. Previous studies and our experimental studies (including ROI masks) SPL subregions that showed activation.

Study name	**SPL1**	**SPL2**	**SPL3**	**SPL4**	**SPL5**	**Other**
Billington et al., (2010)			✓	✓	✓	
Billington et al., (2013)		✓			✓	
Field et al., (2007)	✓			✓	✓	just outside SPL4
Inman, L.A. (2014)			✓	✓		
Jordan et al., (2001)			✓			
Jovicich et al., (2001)			✓	✓		
Ohlendorf et al., (2010)	✓		✓	✓		just outside SPL
Peuskens et al., (2001)			✓	✓		
Vandenberghe et al., (2001)	✓		✓	✓		just outside SPL5
Wolbers et al., (2008)	✓		✓			
Wu et al., (2016)					✓	
Experiment 1	✓	✓	✓	✓	✓	
Experiment2	✓	✓	✓	✓	✓	
Experiment3	✓	✓	✓	✓		
ROI Exp1	✓	✓	✓	✓		
ROI Exp2/3	✓	✓	✓	✓		
TOTAL	9	6	13	12	6	

5.6 Discussion

The Wang et al., (2015) study produced an SPL parcellation using a variety of neuroimaging techniques although the DTI parcellation was used for all analysis in this thesis. This parcellation showed five distinct areas in the left and right hemispheres. By overlapping the key conditions from the three experiments from this thesis we could determine if any of the activation we observed were located in a specific subregion. The functional characteristics of each subregion has also been suggested by Wang et al., (2015) and was looked at in terms of which subregions were activated by the key conditions. Overall, no very focussed patterns emerged; the key conditions activations fell within multiple SPL subregions in both the left and right hemispheres. In the left hemisphere, three conditions (condition 5, *triplet teleporting* and *CD4UpDown*) had activation that spanned all 5 subregions, whereas in the right hemisphere, only *triplet teleporting*'s activation spanned all five subregions. Likewise, for the previous published studies there were multiple SPL subregions that had activation, including outside Wang et al., (2015) listings of the SPL subregions.

The conditions where there was a change in interobject distance between a fixed and moving element (conditions 3, 5 and *CD4UpDown*) had multiple subregions with activation, with condition 5 and *CD4UpDown* spanning the most. This could suggest the assumption that interobject distance requires multiple different populations of neurons and therefore subregions involved in order to calculate interobject distance. However, the *translating_5* condition also had activation across multiple subregions, and it had no change to interobject distance or visual angle.

The individual functional characteristics provided by Wang et al., (2015) appear across a number of different subregions such as: execution, space and vision shape; whereas some individual characteristics are specific to one or two subregions such as imagination, reasoning and language orthography. The functional characteristics from Wang's listing that repeated the most throughout the key conditions of the experiments reported in this thesis were execution, space, vision motion and vision shape. The eleven other published studies were then examined to determine whether their peak activation fell within specific SPL subregions. Again, different peak coordinates, often from the same study, fell within multiple different subregions. When looking at all the results collectively, the left hemisphere had most activation in SPL1, SPL3, SPL4 and SPL5 as the most often subregions to show activation and in the right hemisphere it was SPL3 and SPL4.

SPL3 was the subregion that had the most activation when combining across previous studies and the experimental studies of this thesis, which Wang allocated the functional characteristics of vision motion, space, execution, vision shape, and reasoning. These characteristics provide a good description of the type of studies that had activation within this subregion, in particular vision motion, vision shape, and space, because of the nature of the visual stimuli and task requirements. SPL2 was the subregion with the least activation across the studies considered, and only had activation with the Billington et al., (2013) study and each of our experiments. The functional characteristics Wang attributed were execution and motor learning which could be linked with the Billington et al., (2013) study that involved active steering but, are attributes less obviously related to our results: whereas experiment 1 required an executable task, experiments 2 and 3 required eye fixation from the participant only.

Due to the varied nature of activation across the different subregion in the SPL parcellation proposed by Wang et al., (2015), and the multiple functional characteristics, it appears likely that each of the SPL regions is involved in a variety of functions. With regards to the visual separation hypothesis, the SPL does appear to play an important role but not one that is subregion specific.

We set out in chapter 1 our secondary anatomical question of whether a particular subregion of the SPL selectively activated for visual separation, as well as identifying whether the published studies activation fell within specific subregions. This would also provide a narrow subset of functional characteristic claims that we hoped we would show could be explained by a more general theory of visual separation. The results in this chapter are not encouraging for that project because they may undermine the assumption that specific claims relate to the same sub-region of the SPL. However, we are unable to draw any strong conclusions due to the peak coordinates from the published studies being used in the analysis rather than full activation patterns which might show more overlapping voxels in one SPL subregion. Furthermore, the differences between scanners, hardware, registration methods and anatomical differences between small groups of participants that are generally used in fMRI studies could all have increased the variations between the studies artificially.

Chapter 6 – General Discussion

6.1 Summary of findings

The function of the SPL has previously been undetermined with no consensus reached and conflicting reports from published studies including attentional theories, future heading direction detection theories, and mental rotation. This thesis aimed to test two possible broader hypotheses of SPL function: shifting spatial attention and dividing attention, as well as a unifying theory based on processing of visual separation that was proposed here.

Our first experiment replicated and expanded upon Vandenberghe et al.'s, (2001) study and comprised of a variety of displacing and static conditions that used a fixation cross and cuing circle to identify covert and overt viewing to the participant. The object displacing conditions replicated Vandenberghe et al., (2001) activating the SPL. However, Vandenberghe et al.'s (2001) shifting spatial attention hypothesis was refuted by a key shifting condition (single square displacing) that produced a very low BOLD signal in the SPL. The divided attention hypothesis was not supported because in conditions 6 and 7, varying the amount of divided attention required by the participant did not influence the BOLD signal. However, there was an unexpected result where conditions 6 and 7 produced strong SPL activation that under the visual separation hypothesis would not have been predicted. This is because the BOLD activation would only have occurred in a block design when the visual separation varied during the block. These unexpected results were further investigated in experiment 2 where the ‘jumping/teleporting’ nature of the visual stimuli was considered in comparison to the same visual stimuli that had smooth translation. The findings of experiment 2 showed that the ‘jumping’ displacement of the visual stimuli in experiment 1 was likely to make the SPL recalculate visual separation at each new location, whereas adaptation to the fixed visual separations present in the stimuli occurred in the smoothly translating conditions. The single object smoothly translating condition, did not activate the SPL which was also consistent with the visual separation hypothesis.

The third experiment provided a further exploration of visual separation when divided into two components, interobject distance and visual angle, to determine if one or both were required for SPL activation. The findings from this experiment suggest that the SPL could be sensitive particularly to the relative changes in interobject distance and/or visual angle. When comparing these experimental results against a SPL parcellation from Wang et al., (2015), which had identified five subregions, there were several subregions that activated during the tasks. There was however, no obvious or strong pattern that emerged. This was consistent with the SPL having multiple somewhat distributed functions, including visual separation: which, whilst it appears to be important in SPL is not tied to a particular subregion.

6.2 Relating findings to the literature

We have shown that visual separation is made up of changes in interobject distance and visual angle and suggested that relative changes to interobject distance and/or visual angle are important in the SPL. Referring back to the published studies reviewed in chapter 1 which also had coordinates identifying SPL activation, and concentrating on the visual stimuli in relation to the two components of interobject distance and visual angle, could provide further support for this.

The studies that utilized similar visual stimuli that contained a textured ground plane, a solid sky plane and road edges found activation in the SPL (Billington, Field et al., 2013, Billington, Wilkie, et al., 2010; Field et al., 2007; Inman, 2014). The road edges movement produced changes in interobject distance due to the winding nature and converging perspective at the horizon level. Removing the road edges from the textured ground plane left optic flow only, this suggests that the reduced SPL activation was because the textured ground plane flow did not contain any fixed elements and therefore there would be no changes in interobject distance to perceive. Furthermore, in the control condition, where there was a horizontal road, there was minimal activation in the SPL which in relation to visual separation could be due to the fixed width of the road creating no interobject distance changes. In all these conditions, the horizon line could also be viewed as a fixed point for visual angle changes in a polar coordinate system to be calculated where changes to visual angle would be observed in the road conditions that had a forward trajectory but would have minimal change in the horizontal road conditions because the road curvature changes would be less prominent.

There were five papers that included a fixation cross/point throughout their trials (Jovicich et al., 2001; Ohlendorf et al., 2010; Peuskens et al., 2001; Vandenberghe et al., 2001; Wu et al., 2016). A fixed point against moving elements or objects creates the changes in interobject distance and also visual angle because the fixed point provides the basis for differences within a polar coordinate system. In each of these five papers, simple stimuli e.g., square, dot or ball were used whereas in two additional papers, mental imagery and rotation of complex shapes were used which also activated SPL (Jordan et al., 2001; Wolbers et al., 2008). In Jordan et al., (2001) study participants were expected to mentally rotate a letter or object and compare it to an original (the two items were side by side on the screen), and in Wolbers et al., (2008) study they used objects for a spatial updating task. Both of these studies had more complex stimuli and also required changes that were imagined rather than physical. For the Jordan et al., (2001) study the original letter/object was on the screen and the mental rotation required would create changes in interobject distance, visual angle changes could be relative to the fixed original letter/object. For the Wolbers et al., (2008) study the visual stimuli comprised of a ground plane containing white dots and a solid black sky plane, this made the horizon line evident and could provide the reference for the mentally extrapolated changes in visual angle and interobject distance of the objects and ground plane dots.

Each of the above studies reviewed in chapter 1 can be explained by changes to visual separation with interobject distance and visual angle changes when using a horizon line as a reference point as well as the more obvious fixation point/cross.

6.3 Multiple objects tracking studies

Multiple object tracking studies usually involve identical visual stimuli that move, where a subset of to-be-tracked stimuli is shown to the participant who then has to track them within the full set of moving stimuli before the movement stops and one object is highlighted, requiring the participant to identify whether that object was in the original subset (Howe, Horowitz, Morocz, Wolfe, & Livingston, 2009). Tasks such as these include many visual separation changes in the visual stimuli that produce SPL activation. A study by Howe et al., (2009) showed that activation in the SPL is dependent of the amount the participant is attending to the stimuli; attention is an important consideration for any theory of parietal lobe function.

Jovicich et al., (2001) was another multiple object tracking study that activated the SPL. When we overlaid the peak coordinates over the Wang et al., (2015) SPL parcellation there were two sets of coordinates that appeared in SPL3 and SPL4 subregions. Jovicich et al., (2001) also reported activation in a passive viewing condition compared to a fixation condition, suggesting a replication of this study would be needed to determine whether multiple tracking studies with passive viewing of moving stimuli and a fixed element do activate the SPL.

6.4 Numerosity and visual separation

We discussed numerosity of visual separations in chapter 4 in relation to the unexpected results for the *translating_5* condition (in experiment 3) where five translating dots activated the SPL, but a triplet of squares translating, and a single square translating (in experiment 2) did not activate the SPL. The number of visual separations (interobject distances) between the dots was provided as a possible explanation rather than the number of dots themselves. The number of visual separations between two or more objects increases at a much higher rate as numerosity of objects increases.

A three-mechanism model has been suggested for perception of numerosity that consists of subtizing (numbers up to 4); estimation (intermediate numbers) and texture-density (high density or numerous stimuli) (Anobile, Tomaiuolo, Campana, & Cicchini, 2020). Harvey et al., (2013) study showed that the posterior SPL (at MNI coordinates x23, y-60, z60) showed selectivity for smaller numerosities, with evidence of topographical organisation where clusters of numerosity tuned neurons of small set-sizes e.g. a set-size of 1, or a set size of 2, are clustered together in the cortex. Harvey et al., (2013) also reported that for higher set-sizes there was less cortical area, with tuning width becoming broader at higher set-sizes. It is possible that processing visual separation could be a way of interpreting their results rather than numerosity per se, with topographical organisation according to the number of visual separations. This could be interpreted from the stimuli and procedure because Harvey et al., (2013) used a fixation cross that spanned the whole screen which the authors state allows for more accurate fixation. The visual stimuli were presented close to the centre of the large fixation cross to reduce eye movements; and importantly a new dot pattern of varying numerosities was presented every 750ms in a slightly different location each time – this would produce a perception of displacement of the elements relative to the fixation cross, similar to stimuli reported in Chapter 2. It is feasible that Harvey et al., (2013) and our visual separation hypothesis are compatible because numerosity and visual separation as concepts are closely related, suggesting the possibility that their processing may be interconnected in the brain. A future study could be designed that addressed this notion which incorporated stimuli that independently manipulated factors such as visual separation, set-size and density.

6.5 The unacknowledged influence of fixation crosses in experimental results

As already mentioned, some of the studies that have produced SPL activation also included a fixation point/cross to enable the participant to fixate on a particular place. This is done in a wide range of studies, including behavioural ones, to keep experimental stimuli in fixed retinal locations. An example of this is comparing visual stimuli from Field et al., (2007) *flow* condition and the visual stimuli from Peuskens et al., (2001) study. Both the visual stimuli in the two studies featured a ground plane, which was textured in Field et al., (2007) and a dot field in Peuskens et al., (2001) study. However, there was no fixation point or cross in the Field et al., (2007) *flow* condition and it did not activate SPL, whereas there was a fixation point and two peripheral dots either side of the point in the Peuskens et al., (2001) study and they observed activation in the SPL. The nature of the textured ground plane in Field et al., (2007) study also prevented interobject distance and visual angle perceptions relative to the horizon line. It is likely that the SPL activation in the Peuskens et al., (2001) study was caused by relative motion between the ground place and the fixation. Our findings suggest that the fixation point is often task-relevant in that it influences which brain areas are engaged by a task, even if the relevancy is unintended. Specifically, any experimental conditions that comprises of translating or displacing stimuli against a fixation point/cross (or other fixed element of the stimuli) will activate the SPL. This can occur when the purpose of the experiment is not related to visual separations between a fixed and moving element, subsequently leading researchers to determine the SPL activation to be potentially attributed to the mental process being investigated, when it may simply be related to the relative changes of visual separation. An example of this is working memory studies that use a fixation point/crosses such as Thomas, King, Franzen, Welsh, Berkowitz, Noll et al., (1999) who used a fixation cross throughout their study and reported SPL activation. The visual stimuli also consisted of other fixed elements within the stimuli, similar to conditions 3 and 5 in experiment 1 and Vandenberghe et al., (2001) which all had fixed and moving elements that made up the visual stimuli used in the studies. Any changes that are made to visual separation/angle within the stimulus could cause activation in the SPL. This can also be observed within presentation and delay phases of working memory studies where the stimuli alternate between a single fixation point/cross then multiple objects before a judgement were required by the participant (e.g. Pessoa, Gutierrez, Bandettini & Ungerleider, 2002; van der Ham, Raemaekers, van Wezel, Oleksiak, & Postma, 2009). The perception of displacement due to stimuli being present and then disappearing could suggest that the SPL activation in such studies is caused in the same way as the shifting stimuli in experiment 1. In many experimental paradigms, to ensure that the fixation point/cross is not directly influencing SPL activation it may be prudent to run the tasks with and without a fixation cross to determine whether the BOLD signal significantly changes, although this would of course be time-consuming to do.

Further exploration into the relevance of fixation points/crosses and other fixed elements within visual stimuli that also comprises of moving objects is needed. We propose that replications of the visual stimuli used in some of the published studies highlighted earlier in this thesis to be conducted with and without a fixation point/cross to determine whether the proposed visual separation theory activates the SPL in experiments where this was not the intended focus. This would provide information for different tasks types: using smooth pursuit eye movements (Ohlendorf et al., 2010), optic flow (Peuskens et al., 2001), motion-tracking (Jovicich et al., 2001b), and visuospatial attention (Wu et al., 2016) alongside the shifting spatial attention (Vandenberghe et al., 2001) replication from experiment 1.

6.6 Bálint’s Syndrome

Bálint’s syndrome is named after Rezsö Bálint, a physicist, who in 1909 published a paper explaining the vision difficulties experienced by a patient who had bilateral parietal lesions (Bálint, 1909 cited in Chechlacz & Humphreys, 2014). Bálint’s syndrome is stated to comprise of three different symptoms: simultanagnosia (the inability of being able to see more than one object at a time); optic apraxia (difficulties with reaching for objects); and ocular apraxia (being unable to make voluntary saccades to objects) (Rizzo & Vecera, 2002). Bálint’s syndrome is comparatively rare resulting mainly in case studies on single patients (Chechlacz & Humphreys, 2014).

There are noteworthy parallels between our key condition of experiment 1, where the fixation cross is removed leaving a single square, and simultanagnosia. The key condition did not activate SPL, which could suggest, in a broad sense, that the SPL engages whenever two objects are perceived simultaneously; whilst in simultanagnosia, patients who have damage to their SPL have the inability to perceive more than one object at a time.

A recent case study found that due to SPL damage in both hemispheres a patient was impaired at judging the relative locations both within and between objects they were shown (Vialatte, Yeshurun, Khan, Rosenholtz, & Pisella, 2020). We have shown that the interobject distance between two or more objects is important to the SPL and this neuropsychological data from Bálint’s syndrome patients provides further support that the SPL is involved with processing such spatial relationships between objects.

6.7 Limitations

A potential limitation to our experiments relates to the thresholding that we used. The initial voxelwise threshold was set to 3, with a cluster p threshold <0.05, for the group level analysis. The ROI masks used individual thresholds that were adjusted per participant, but the starting point for each participant was the same as above. Cluster extent thresholding is a popular method of thresholding that passes clusters above a certain critical size (Woo, Krishnan, & Wager, 2014). However, passing the cluster threshold only indicates that there is a significant activation of one or more voxels somewhere within the cluster without specifying where (Woo et al., 2014; Yeung, 2018). Furthermore, cluster thresholding has been criticized as sometimes leading to an inflated false positive rate (Eklund, Nichols, & Knutsson, 2016); this was one reason why we raised the voxelwise component of the thresholding method from the default z=2.3 to z=3.0. Recommendations for using cluster-extent thresholding include that a more strict *p* value could be used e.g. *p*<0.001 and that inference across multiple anatomical regions are limited (Woo et al., 2014); and for readers to note the thresholds used for different elements of analysis (Yeung, 2018).

Another limitation of this study was the differences between the Wang et al., (2015) SPL parcellation, which was used to see whether our experimental data, and the peak coordinates from published studies fell within specific subregions of the SPL, and the Harvard-Oxford Cortical Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) probabilistic maps used in creating the ROI masks for our experimental data. Whilst some overlap of the parcellation and atlas was present, it was evident from our ROI masks (which comprised of relevant voxels with at least a 20% probability of being in SPL according to the Harvard-Oxford Cortical Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006)) that SPL5 from Wang et al., (2015) listing had the least number of voxels with activation out of the subregions. The atlas and our ROI masks both included voxels that were superior to the SPL parcellation subregions. This produces questions relating to the differences in the anatomical area of SPL provided by both the atlas and SPL parcellation subregions which would need further investigation. It is worth noting that the Wang et al., (2015) study used the Colin27 template brain (Holmes, Hoge, Collins, & Evans, 1996) which is a template that contains an average of 27 scans from the same person, whereas the Harvard-Oxford Cortical Atlas (Desikan et al., 2006; Frazier et al., 2005; Goldstein et al., 2007; Makris et al., 2006) is part of the FSL package and was made by aligning images from 37 participants to the MNI152 template which is the average of anatomical images from 125 adults (Jenkinson & Chappell, 2018) suggesting that some anatomical differences may have influenced our results.

We have also reported that a scanner upgrade took place between experiments 1 and 2/3. The timing of the upgrade was not available at the time of planning of the first experiment or during the planning stages for experiments 2 and 3 resulting in a difference of scanner properties and a change in participants that occurred between the first and subsequent experiments. This limited the ability to directly compare across all experiments and is why the ROI and data for experiment 1 were kept separately from experiments 2 and 3. Ideally, we would have used the same participants and scanner type throughout all experiments to enable direct comparability.

6.8 Future experiments

A number of potential experiments are suggested by our findings. In particular, further investigation into the translating conditions when numerosity increases would be valuable. An experiment could be conducted that replicated the triplet findings from experiments 2 and 3 and then expanding upon the *translating_5* condition by introducing different shapes configurations as well as having another condition with more objects (see Figure 6.8.1). The visual stimuli would smoothly translate as it did in previous experiments with a fixed interobject distance and visual angle. This proposed experiment would provide further information relating to numerosity of objects as well as numerosity of visual separation because the different *dots in a line* conditions (3, 4 and 5 dots) reduces the number of visual separations relative to the *shape* conditions (*3_triangle*, *4_diamond* and *translating_5*). If the number of visual separations in the configuration is more important than the number of objects, then activation is SPL for the line configurations will be lower than for the shape configurations.

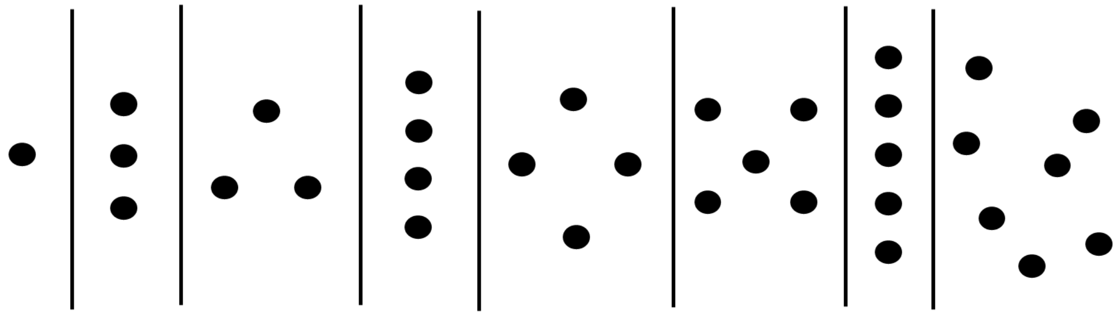


Figure 6.8.1. Eight panels showing different configurations of visual stimuli of a potential smooth translation experiment incorporating line and shape configurations to vary the number of visual separations.

Another future experiment would be to investigate different configurations of patterns to further isolate and explore selective SPL activation related specifically to changes in visual angle, and how these interact with the number of objects present. To isolate visual angle a different configuration of visual stimuli is needed. Using the *CD4Rotate* visual stimuli as a base, different numerosities of dots that travel around a central dot keeping interobject distances constant will help determine the nature of changes to visual angle only in the SPL (see Figure 6.8.2.). Activation would be expected in the SPL based upon the results of the *CD4Rotate* condition, but the experiment will also explore whether the numerosity of dots makes a difference. The numerosity of dots would be expanded beyond those shown in Figure 6.8.2. to include higher values such as 5 and 8.

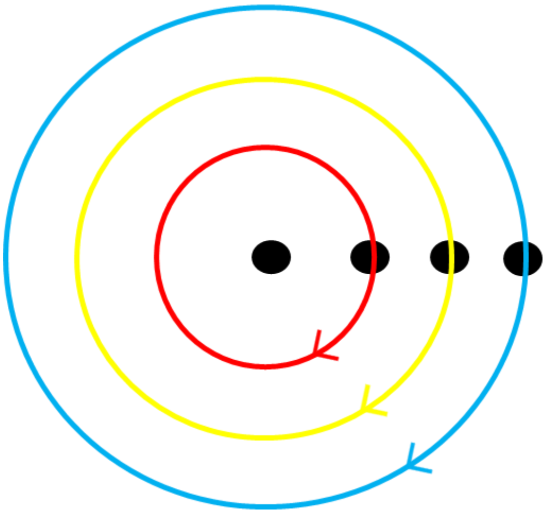


Figure 6.8.2. A proposed example of changes to visual angle only with increasing dot numerosity. A static central dot, with a second dot (following the red path), a second condition would include an additional dot (yellow path), a third condition would include another additional dot (blue path) and so on.

Isolating and further exploring interobject distance would be another future experiment and can be achieved when the objects stay at the same visual angle but the distance between the objects increases or decreases. The distance changes can vary to include a static and one moving dot, two dots moving in opposite directions along the same visual angle and a central dot with two dots flanked either side and moving in opposite directions along the same visual angle (see Figure 6.8.3.). We would predict activation in the SPL due to the changes in interobject distance and these conditions would allow us to keep visual angle constant and examine interobject distance in isolation. We would examine how activation level in SPL is modified by different numbers and patterns of interobject distance changes, including such factors as the presence or absence of symmetry

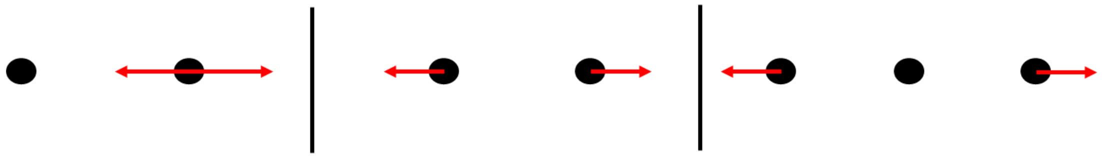


Figure 6.8.3. Three panels showing varying types of interobject distance changes. The dots with red arrows show movement and direction of movement, whereas the black dots without arrows are static.

6.9 Conclusion

There has not been any consensus reached regarding the function of the SPL despite numerous studies reporting activation within this brain region. We have shown that two attentional theories: shifting spatial attention and divided attention that might have explained activation in the SPL are less consistent with the data than an alternative theory based on the representation of visual separation, specifically relative changes to interobject distance and/or visual angle. Whilst visual separation between objects appears to be important in the SPL, it is not localised within a specific SPL subregion, but rather across multiple regions which is consistent with a potentially multifunctional SPL brain region.

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