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MAPPING BRAIN ACTIVITY DURING LOSS OF SITUATION AWARENESS: an EEG investigation of a basis for top-down influence on perception

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PRÉCIS / SHORT ABSTRACT

Loss of SA was enforced in two tasks requiring identification of target items (respectively, abstract concepts and urban "threat"). EEG recording and source-localization with sLORETA shows rapid co-activity of regions for visual perception and those with high-order duties. This may offer a basis for top-down effects on level 1 SA.

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Running head: Brain activity in loss of SA

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ABSTRACT

Objective: The objective was to map brain activity during early intervals in loss of Situation Awareness (SA) to examine any co-activity in visual and high-order regions, reflecting grounds for top-down influences on level 1 SA.

Background: Behavioural and neuroscience evidence indicates that high-order brain areas can engage before perception is complete. Inappropriate top-down messages may distort perception during loss of SA. Evidence of co-activity of perceptual and high-order regions would not confirm such influence but may reflect a basis for it.

Methods: SA and Bias were measured using QASA (Quantitative Analysis of Situation Awareness) and brain activity recorded with 128-channel EEG (electroencephalography) during loss of SA. One task (15 participants) required identification of a target pattern and another task (10 participants) identification of “threat” in urban scenes. In both, the target was changed without warning, enforcing loss of SA. Key regions of brain activity were identified using source localization with sLORETA 150-160msec post-stimulus-onset in both tasks and also 100-110msec in the second task.

Results: In both tasks, there was significant loss of SA and Bias shift ($p \leq .02$), associated at both 150 and 100 msec intervals with co-activity of visual regions and prefrontal, anterior cingulate and parietal regions linked to cognition under uncertainty.

Conclusion: There was early co-activity in high-order and visual perception regions that may provide a basis for top-down influence on perception.

Application: Co-activity in high- and low-order brain regions may explain either beneficial or disruptive top-down influence on perception affecting level 1 SA in real-world operations.

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MAPPING BRAIN ACTIVITY DURING LOSS OF SITUATION AWARENESS: an EEG investigation of a basis for top-down influence on perception

Effective interaction with the external environment requires that salient aspects are processed appropriately to produce or maintain good Situation Awareness (SA) (Adams, Tenney, & Pew, 1995; Endsley, 1995, 2000, 2013; Durso & Sethumadhavan, 2008; Parasuraman, Sheridan, & Wickens, 2008; Patrick & Morgan, 2010; Wickens, 2008). Complementary theoretical approaches define SA either as a "*state of knowledge*" about a situation (Endsley, 2013) and/or in terms of the *processes* for building that knowledge (Durso & Sethumadhavan, 2008), encompassing both explicit and implicit understanding (Durso, Rawson, & Girotto, 2007). The loss of SA, especially in challenging operational environments such as combat, transport, fireground or medical situations may precipitate critical errors with serious consequences (Borghini, Astolfi, Vecchiato, Mattia, & Babiloni, 2012; Catherwood, Edgar, Sallis, Medley, & Brookes, 2012; Klein, Calderwood, Clinton-Sirocco, 2010; Schulz, Endsley, Kochs, Gelb, & Wagner, 2013). Further investigation of the psychological dynamics underlying loss of SA is of paramount importance.

Understanding of these dynamics has been achieved by the convergence of behavioural and neuroscience evidence. Neuroergonomic research (Parasuraman, 2003; Parasuraman &Wilson, 2008) using functional Magnetic Resonance Imaging (fMRI) and Electroencephalography (EEG) has identified brain response linked to behavioural aspects of SA, such as the association between activity in Prefrontal Cortex (PFC) or the *theta* EEG band and cognitive workload (Berka, et al., 2007; Borghini, et al., 2012; Brookings, Wilson, & Swain, 1996; Dussault, Jouanin, Philippe, & Guezennec, 2005; French, Clarke, Pomeroy, Seymour, & Clark, 2007; Lei & Roetting, 2011; Parasuraman, Warm, & See, 1998; Savage, Potter, & Tatler, 2013; Sterman & Mann, 1995; Wilson, 2000). EEG activity also reflects aspects of team SA (Stevens, Galloway, Wang, & Berka, 2012). Investigation of behaviour linked to SA and corresponding brain activity may also provide deeper insights into another key issue regarding SA– namely, “top-down” influence on perception (level 1 SA). Loss of SA may be associated with perceptual lapses or impairment due to top-down factors such as prior memory or expectation (Durso et al., 2007; Durso & Gronlund, 1999; Endsley, 2013). Investigation of the associated brain dynamics may advance understanding of this issue for the following reasons.

Most models of SA cite a processing trajectory from perception (level 1 SA) to cognitive integration (level 2) to projection (level 3), but it is acknowledged that top-down factors influence all levels of SA (Durso & Gronlund, 1999; Endsley, 2013). Individuals make more errors if situations do not fit expectations (Taylor, Endsley, & Henderson, 1996) and loss of SA may involve distortion of perception by faulty top-down processing. For example, in the Mt. Erebus aircraft disaster, the flight-crew’s expectation based on faulty flightpath data may have caused visual information about location to be overlooked (Mahon, 1981) and in the Storm King Mountain wildfire tragedy, an overworked commander may not have perceived a shift in wind conditions (Sallis, Catherwood, Edgar, Brookes, & Medley, 2013; Useem, Cook, & Sutton, 2005).

Such cases resonate with neuroscience evidence indicating that information-processing in the brain does not follow a strictly linear-hierarchical trajectory, but may involve bi-directional (“re-entrant”) communication between high-order cortical regions and low-order perceptual regions. There is ongoing discussion about the nature and timing of these brain dynamics (e.g., Fu, Fedota, & Parasuraman, 2012; Rauss, Pourtois, Vuilleumier, & Schwartz, 2012; Rauss, Schwartz, & Pourtois, 2011; Theeuwes, 2010), but high-order regions may rapidly transmit “predictive and adaptive” coding about a situation, based on expected input, learned contingencies or affective factors that can modulate perceptual response (Bar, 2003; Damaraju, Huang, Barrett, & Pessoa, 2009; Dambacher, Rolfs, Göllner, Kliegel, & Jacobs, 2009; Delorme, Rousselet, Macé, & Fabre-Thorpe, 2004; Furmanski, Schluppeck, & Engel, 2004; Gilbert & Sigman, 2007; Hegdé, 2008; Kelley, Rees, & Lavie, 2013; Paradiso, 2002; Poghosyan & Ioannides, 2008; Rauss, et al., 2011; Schettino, Loeys, Delplanque, & Pourtois, 2011; Summerfield & Egner, 2009). Indeed, expectation alone can excite visual cortex (Grill-Spector & Malach, 2004). Such top-down influence on perception may be critical during loss of SA. Establishment of SA or efforts to recoup lost SA may enlist top-down processing, but if premature or inappropriate, this could distort perception of the situation. For example, faulty expectation may have elicited visual focus on an irrelevant cockpit signal during loss of a 1972 Eastern Airlines flight (National Transportation Safety Board, 1973). “Looked but fail to see” accidents (Langham, Hole, Edwards, & O’Neil, 2002) may also be due to poor visual processing of the traffic environment if inconsistent with expectations.

It may thus advance understanding of loss of SA to establish if high-order brain regions are co-opted while perceptual coding is actively proceeding. This issue is addressed in the current investigation. The approach is to build SA then enforce its loss in tasks requiring decisions about a target item. EEG source analysis will reveal if loss of SA is associated with concurrent activity in brain regions with high-order duties and those for perceptual (visual) processing. Parallel co-activity of these regions is not direct evidence of their interaction. Nevertheless it reflects potential conditions for such interaction, compared to a strictly linear sequence whereby perception subsides before high-order processing occurs.

Combining theoretical approaches (Durso & Sethumadhavan, 2008; Endsley, 2013; Patrick & Morgan, 2010; Wickens, 2008), SA will be explored as a state of knowledge in relation to brain activity. As noted, there is already relevant neuroergonomic evidence on brain response under high cognitive-load conditions associated with loss of SA (Parasuraman et al., 2008). This evidence mostly derives from Event-Related-Potentials (ERPs) and/or EEG spectral analysis (e.g., P300) (Foxe & Simpson, 2002; Makeig, et al., 2002; Philiastides & Sajda, 2006; Rousselet, Husk, Bennett, & Sekuler, 2007). These methods use summated estimates of brain activity, but fMRI studies have more precisely mapped sources of brain activity associated with SA: for example, in ACC (anterior cingulate cortex) and PFC (prefrontal cortex) during driving or aviation performance (Calhoun & Pearlson, 2012; Causse, Dehais, Péran, Sabatini, & Pastor., 2013; Causse, et al., 2013b; Peres, et al., 2000). fMRI however has slow temporal resolution (Raichle, 1998) and may not capture the early processing dynamics of interest here. EEG with source localization is better able to achieve this (Foxe & Simpson, 2002) and has been used to identify sources of brain activity under challenging conditions such as microgravity (space) flight (Brümmer, et al., 2011; de la Torre, et al., 2012; Schneider, Brümmer, Carnahan, Dubrowski, Askew, & Strüder, 2008).

The current investigation will map brain activity during loss of SA using EEG source analysis with the sLORETA algorithm (see Method). This method will estimate sources of brain activity in terms of Brodmann Areas (BAs), useful markers of circuitry for brain functions (Amunts, Schliecher, & Zilles, 2007). As in other studies of SA (e.g., French et al., 2007), ERPs (averaged EEG signals) will not be used, since as noted above, they may mask the early co-activity of interest here. Unaveraged EEG data may more directly reflect the brain dynamics of interest (Philiastides & Sajda, 2006; Rousselet, Husk, Bennett, & Sekuler, 2007).

Brodmann areas are not isolated modules, but typically contribute to wider networks and are used here in this respect (e.g., BA17 and BA20 are both on the visual pathways: Table 1). Neuroimaging methods reveal modularity for some brain functions (Downing, 2008; Downing, Liu, & Kanwisher, 2001) but it may be more informative to investigate brain operations on a broader scale that can reveal connectivity of processing (Poldrack, 2012). For example, an fMRI study showed that novice pilots display more distributed cortical activity than experienced pilots, reflecting differential expertise (Peres et al, 2000). Recording broad-scale individual maps of brain activity may thus provide clues to global brain dynamics during loss of SA. The aim here is therefore not to simply identify active brain regions during loss of SA, but to examine any *co-activity* of regions with high-order duties and those for perception. Such co-activity may indicate a basis for top-down influence on perception.

<Insert table 1 about here>

During loss of SA many brain regions may be engaged with variations across situations and individuals. Nevertheless to address the central question of whether areas with high-order duties are aroused while perception is progressing, the following regions are of interest, based on prior evidence of their roles in these functions (see Table 1a and 1d for references).

If visual perception is actively occurring, multiple regions may be engaged (Grill-Spector & Malach, 2004; Tootell, Hadjikhani, Mendola et al., 1998). These include: primary visual cortex (V1 or BA17), ventral and dorsal areas for higher-level visual analysis (BAs 5,18,19,20, 37), retrosplenial cortex (BA29-30) for visual scene integration and perirhinal cortex (BA35-36) for complex visual binding and figure-ground perception (see Table 1a).

For high-order cognitive processing, many brain regions are of potential interest, but efforts to recoup lost SA must employ regions involved in cognitive integration (level 2 SA) and possibly projection (level 3 SA). The brain activity for these levels is not easily distinguished, but on the basis of prior evidence, numerous frontal, anterior cingulate and parietal cortical regions may predictably be implicated for both (see Table 1d for a representative list with references). Loss of SA may especially enlist regions known to be active with cognitive uncertainty or ambiguity, low confidence, error and the need to reverse responses. These include: BA9 and BA46 (Dorsolateral PFC), BA11 (Orbitofrontal cortex), BA 47 (Orbitofrontal/ Ventrolateral frontal cortex), BA24, 32 and 33 (ACC) and BA7 (Superior Parietal Lobule) (see Table 1d for references). The link between activity in these areas and loss of SA has not been specifically examined to date and evidence of their rapid involvement during active perception could afford new insights into brain conditions associated with top-down influences during loss of SA.

The interval of interest for EEG analysis is that encompassing active perceptual processing of the situation prior to response on each trial. Visual perception involves activity and co-activity in multiple regions (Table 1a) for up to hundreds of milliseconds (Paradiso, 2002). Coarse visual coding is complete by 80-90msec post-stimulus (or sooner), basic stimulus classification by 75-120msec and registration or identification of the "gist" of a visual context by 150msec (Bar, 2003; Delorme, et al., 2004; Foxe & Simpson, 2002; Rauss et al., 2011; Hegdé, 2008; Jolij, Scholte, Gaal, Hodgson, & Lamme, 2011; Schettino et al., 2011; Thorpe, Fize, & Marlot, 1996). Decision-related visual processing can require 250msec (van Rullen &Thorpe, 2001) and activation of visual cortical areas can continue for 400msec before a motor response or conscious reporting of visual input (Foxe & Simpson, 2002; Jolij et al., 2011). In consideration of these timeframes, 150msec post-stimulus-onset was selected to represent a phase when the basic visual situation has been "sensed", but with ongoing visual processing to achieve a complete perceptual representation of the situation corresponding to level 1 SA (Endsley, 2000; 2013). This provides a justifiable timeframe for determining whether regions for higher-order operations engage during early perceptual processing in loss of SA. Nevertheless if there is evidence of strong arousal of high-order regions at this interval, then an even earlier interval will be explored in Experiment 2.

The approach here offers a relatively novel means for assessing brain response during loss of SA. SA will be established to a criterion level and then loss of SA enforced at the same juncture for all participants. This general approach has been used in a recent study of confusion in reading incongruent text (Durso, Geldbach, & Corballis, 2012). The current experiments involve an abstract “baseline” task and a similar task with more real-world content involving identification of threat in urban scenes. In both tasks the “situation” is defined in terms of target information within a visual field. The essential requirements resemble many real-world situations requiring perceptual and cognitive processing to identify a target item (e.g., decisions about whether symptoms indicate disease). The first task was chosen to be less likely to arouse prior knowledge or expectations than the second which may invoke knowledge about urban crime. This contrast allows assessment of whether high-order regions are aroused during perceptual processing regardless of whether the task is “abstract” or more “real-world”, or instead is more likely in the latter. Both tasks however require at least two levels of SA (Endsley, 1995): participants must perceive the visual information (level 1) and integrate that information to comprehend and hypothesize about the correct target characteristics (level 2). Activity in brain areas for high-order processing would be required to achieve level 2, but the question is whether it occurs during activity for level 1.

The loss of SA may elicit individual differences in response (perseveration, trial-and-error, etc.), but regardless of the strategy, high-order cognitive functions will be required to re-attain level 2 SA. Discriminating brain patterns for different strategies is an issue for future investigation. The aim here is to answer the basic question of whether there is any brain activity consistent with high-order cognitive processing concurrent with perceptual processing. To this end, the analysis will firstly determine if visual perceptual regions are actively engaged and if so, then assess if there is concomitant arousal of regions associated with cognition under uncertainty. It is hypothesized that despite individual differences, such co-activity will be apparent to some extent for all participants in both tasks, but possibly to a greater extent in Experiment 2.

EXPERIMENT 1: BASELINE WISCONSIN CATEGORY LEARNING TASK

This task is a variant of the Wisconsin Card Sorting Task (WCST) (Berg, 1948; Grant & Berg, 1948) employed here as a tool for exploring basic processes linked to loss of SA. The "situation" requires detection of a target "concept" amongst stimulus exemplars involving combination of features across three visual dimensions (colour, shape, line orientation). This requires (a.) *perception* of the elements (colours, etc.) (level 1 SA) and (b.) *cognitive integration* of these for generating hypotheses or responses, with this involving memory and processing to link responses to the feedback on each trial (all relevant to level 2 SA). Once the correct category (= SA) is achieved, this will be changed without warning, occasioning loss of SA which participants then have to reattain. This approach brings all participants to a common reference point for loss of SA and the need to regain it.

METHOD

Sample. Participants were right-handed volunteers from the local student and staff population with no known neurological disorder. The experiment was completed by 23 participants but 8 failed to achieve satisfactory SA and were not included in the final analysis, leaving a sample of 15 participants.

Design. The study was within-participants (all did both phases of the experiment).

Apparatus and stimuli. Participants were presented with a series of computer displays, with each either containing examples of a 'target category' or not, and consisting of four quadrants with one of three possible variations of a visual property. The top left quadrant had one, two, or three lines, the top right quadrant was red, green, or blue, the bottom left quadrant had vertical, horizontal or oblique lines and the bottom right quadrant had a diamond, circle, or square. (See Figure 1.) The 'target category' in Phase 1 was "three lines and red". In Phase 2, the target category was changed without notice to "oblique lines and circle". Phase 2 trials contained the same displays as Phase 1, but the target category was changed.

<Insert Figure 1 about here>

Brain activity was recorded with Electrical Geodesics Incorporated (EGI)™ EEG apparatus consisting of 128-channel HydroCel GeoDesic Sensor Net(s) (with a reference/vertex (C_z) sensor) connected to a wall-mounted NetAmps™ amplifier. The dense geodesic array of the net (Figure 2) optimises accurate recording. The 128 high-impedance electrodes with sponge inserts (with HydroCel saline electrolyte) include eye-blink and eye-movement sensors. The signals from the 128 sensors were sent to a Macintosh computer running Netstation™ software for acquiring, viewing and navigating the data. Further source localization was performed using the GeoSource 2.0™ software that has received both US FDA and European Medical Device Directive clearance (http://www.egi.com/home/385-geosource-fda). See further details below.

<Insert Figure 2 about here>

Procedure. Participants were given instructions about the task and EEG procedure. If consent was given, an appropriate-sized EEG net was applied. Stimulus arrays and instructions were presented on a PC monitor via E-prime™ software, with presentation controlled by E-prime and responses made via the PC keyboard. The net was accurately positioned relative to the vertex point pre-marked on the scalp relative to the nasion, inion and pre-auricular clefts. Prior to testing, scalp impedances were adjusted below 50 kΩ. Testing was in low-light with shielding of electrical cables and equipment.

There were 10 practice and 104 experimental self-paced trials (52 in random order in each phase) with no signal that Phase 2 had begun. To increase task difficulty, there was overlap between category exemplars: each Phase had 26 trials with the correct target and 26 without, but for each Phase, 16 displays had category 1; 16 category 2; 10 both categories and 10 neither category. Each trial began with a fixation marker for 1 to 1.5 seconds (randomised in this range) followed by a display. For each display, participants had to respond to the question: "*This slide represents a member of the target category. T/F?"*. Feedback on correctness of response and reaction time was provided *on each trial* in both phases. Participants could quickly become aware in Phase 2 that their previously correct response was now incorrect. They still may not identify the new category as there are 6 possible pairings of the features and may perseverate with the old concept or try other strategies. The key issue however is whether SA is lost with the target change and QASA[1] scores (see below) allow confirmation of this loss.

Measures of performance. Performance was measured by (a.) QASA scores of SA and Bias (Edgar & Edgar, 2007; Edgar, Catherwood, Sallis, Brookes, & Medley, 2012; Rousseau, Tremblay, Banbury, et al., 2010) and (b.) associated patterns of EEG activity.

QASA Analysis. QASA is based on a signal detection approach (Green & Swets, 1966; Stanislaw & Todorov, 1999) and calculates (a.) Situation Awareness (SA) as Knowledge (how well true information is discriminated from false) and (b.) the Bias applied to the information (tendency to accept or reject information). *Yes/no* responses on "signal" trials (with target) and "noise" trials (without target) provide the proportion of *hits* (correct target identification) and *false alarms* (incorrect identification) to calculate: (a.) SA in terms of A', a "Knowledge" score (corrected for chance or guessing) and (b.) B", a Bias score, both re-scaled from -100 to +100. The computation for these scores (see Stanislaw and Todorov, 1999: page 142) is:

$$A' = 0.5 + \left[\text{sign}(H-F) \frac{(H+F)2+|H-F|}{4max(H,F) - 4HF} \right]$$

$$B'' = \text{sign}(H-F) \frac{H(1-H)-F(1-F)}{H(1-H)+F(1-F)}$$

(where *H*= hit rate and *F* = false alarm rate and *max (H,F)* = either *H* or *F*, whichever is greater). Higher SA scores reflect better SA, with scores below zero misguided or false SA. "Positive" Bias scores (above zero) reflect the tendency to reject information (conservative bias), "negative" scores to accept information (liberal bias) and zero scores no bias. Standard parametric signal detection measures (*d'* and ß) were not used as the data may not meet the assumptions. A' and B'' are more robust and suitable for small samples (Verde, Macmillan, & Rotello, 2006). A' is conceptually related to "% correct" (Pastore, Crawley, Berens, & Skelly, 2003), enabling comparison with SA measures such as SAGAT (Endsley, 1987).

EEG recording and Source Localization methods. Using the 128-channel apparatus (see above) and Netstation software, EEG was recorded at a 250 Hz sampling rate. For subsequent source analysis, only one sample at 150msec was needed, but a 10msec band (150-160msec: providing 2.5 samples on average) was employed to increase stability while still capturing rapid, early response.

The raw scalp data were initially processed by the software in the following respective operations: ***filtering*** (with notch filter centred on 50Hz to eliminate UK mains noise); ***segmentation*** of the recording into epochs linked to the experimental "events" (stimulus onset and offset, trials, etc.); ***automatic artifact detection*** (identification of channels and segments likely to involve eye blinks or movements, etc.); ***bad channel***

(electrode) replacement (replacement of bad channel data with interpolated data from neighbouring channels); ***ocular artifact removal*** (using data from eye blink and eye movement electrodes to remove affected data segments, according to an eyeblink threshold of 14mV/ms, with separate algorithms for eye blinks and movements based on the Eye Movement Correction Procedure: Gratton, Coles, & Donchin, 1983; Electrical Geodesics Inc., 2006); ***artifact detection "overwrite"*** of all previous bad channels/segments; ***further bad channel replacement*** after this overwrite; ***averaging; average re-referencing*** (using Polar Average Reference Effect or PARE correction with spherical spline interpolation to estimate a true zero reference value for the whole brain) and ***baseline correction*** with respect to the level of activity 100msec before stimulus onset. Then the processed data were analysed with ***GeoSource 2.0*** software (E.G.I., 2011) using the following computations to estimate sources of brain activity and map these to Brodmann Areas.

Source localization employed the computations implemented in the GeoSource 2.0 software. This involved both a ***forward head model*** (assumptions about transmission from the dipoles/source locations to the scalp electrodes) and an ***inverse solution*** (best estimate for the sources based on measured scalp activity). Geosource 2.0 offers a dense dipole set to represent "average" cortical space estimated by Montreal Neurological Institute MRI data (E.G.I., 2011) (see Figure 3), but the *forward-head model* for source localization used the ***Sun-Stok4-Shell Sphere model*** representing brain, cerebrospinal fluid, skull, and scalp– a commonly used approach for computational efficiency (Michel, Murray, Lantz, Gonzalez, Spinelli, & de Peralta, 2004). The inverse solution used the ***MNLS*** *(minimum norm least squares) inverse method*, a mathematical "least-squares" procedure providing the best solution for the sources of the EEG scalp data. It has a bias however towards superficial and weak sources so the ***sLORETA*** (standardised low-resolution electrical tomography) constraint was employed to standardize amplitude (*current density*) for both superficial and deep sources (Pasqual-Marqui, 2002; see below). Finally to remove distortion from small "noise" variations, a further correction, the ***Tikonov (1 x 10 and -2)*** *regularization strategy* was applied. The resulting data are an estimate of sources of brain activity (with amplitude reflected in the *standardized current density estimates*). The ***Statistical Extraction Tool*** in the Geosource 2.0 software was employed for mapping to left and right hemisphere Brodmann Areas and the Hippocampus (90 regions total) and for calculating "mean amplitudes" of activity (mean *standardized current density estimates*) in these regions on each trial block.

Source localization algorithms can only provide approximations of brain activity. Nevertheless, sLORETA is superior to previous algorithms such as LORETA (Pascual-Marqui, 2002), with zero localization error in noise-free simulations (Michel, et al., 2004; Pasqual-Marqui, 2002; Sekihara, Sahani, & Nagarajan, 2005) and better performance than other algorithms in the presence of noise (Abe, Ogawa, Nittono, & Hori, 2008; Pascual-Marqui, 2002), provided signals are relatively distinct (Wagner, Fuchs, & Kastner, 2004). Further validation comes from convergence of intracranial EEG and sLORETA (and LORETA) solutions for scalp EEG in localizing epileptogenic zones (Maillard, Koessler, Colnat-Coulbois, Vignal, Louis-Dorr, & Vespignani, 2009; Ramatani, Cosandier-Riméle, Schulz-Bonhage, Maillard, Zentner, & Dümplemann, 2013; Rullmann, Anwander, Dannhauer, Warfield, Duffy, & Walters, 2009; Stern, et al., 2009; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002; Zumsteg, Friedman, Wennberg, & Wieser, 2005). Additional validation for EEG with sLORETA derives from close correspondence with MRI, fMRI and PET data, including for deep sources such as the hippocampus (Cannon, Kerson, & Hampshire, 2011; Maillard et al., 2009; Olbrich, Mulert, Karch, et al., 2009; Ramatani et al., 2013).

sLORETA (and LORETA) are capable of identifying regions active in visual-perceptual and cognitive processing, including visual cortical, ACC and frontal areas of interest here (Lorenzo-López, Amendo, Pascual-Marqui, & Cadaveira, 2008; Ocklenburg, Güntürkün, & Beste, 2012; Olbrich et al., 2009). Of particular value is the capacity of sLORETA to identify sources for top-down control (Cannon, Kerson, & Hampshire, 2011; Li, Yao, & Yin, 2009) and to discriminate early and late visual regions (Kimura, Ohira, & Schröger, 2010; Schettino, Loeys, Delplanque, & Pourtois, 2011).

These considerations indicate that the EEG methods will allow valid identification of brain activity in visual cortical regions and frontal-cingulate areas for high-order processing.

RESULTS

Firstly the QASA analysis and then the corresponding EEG data are considered.

QASA results. The QASA analysis provided SA and Bias scores for trial blocks (20 trials per block). The *pre-change block* at the end of Phase 1 and the *change block* at the start of Phase 2 are of most interest to determine if SA was attained during Phase 1 and then lost in Phase 2.

A criterion of ≥70 SA by the end of Phase 1 (*pre-change block*) was applied, since high initial SA was needed to study the outcomes occasioned by its subsequent loss in Phase 2. Eight participants failed to achieve this and were excluded from further analysis. The remaining 15 participants, by the end of Phase 1 on the *pre-change block*, showed a mean SA of 90.33 (SD 10.56) and Bias scores ranging from -100 to +100. All 15 participants showed loss of SA on the *change block* at the start of Phase 2, with mean SA of 44.55 (SD 29.07), a significant decline from the *pre-change block* scores: t (14) = 7.300, p <.001, d = 2.31. All participants also showed a Bias shift on the *change block*: 10 becoming more positive (conservative) and five more negative (liberal) with a mean *percentage change* in Bias from the *pre-change block* (disregarding direction of change) of 103.46% (SD 25.01), significant compared to no-change (0%): t (14) = 16.024, p <.0001, d = 4.14. The participants thus showed significant loss of SA and shift in Bias with the target change.

The next step was to use the EEG data to map corresponding brain activity during the loss of SA for these 15 participants.

EEG activity with Loss of SA on the Change Block in Phase 2. Each EEG trial block had 10 trials matched to respective QASA blocks. The amplitude of EEG activity with loss of SA on the *change block* was estimated in terms of the *standardised current density estimates* provided by the Geosource 2.0 software with sLORETA (see Method). The software calculated the mean *standardised current density estimates* for the EEG samples from each trial and computed the mean of these estimates for the respective trial blocks for each Brodmann area. As noted, areas of most interest are those identified from prior research as having key roles respectively in visual perception and high-order cognitive functions (Table 1a and d, respectively).

The first question is whether there was evidence of active visual perception on the *change block*. All 90 areas (left and right BAs and Hippocampus) were ranked by *mean standardised current density estimates* on the *change block*.[2] LBA17 and/or RBA17 (V1, primary visual cortex) were the most active (highest-ranked) region(s) for six participants and highly active for others- for example, being in the top 20% of ranked areas for 12 participants. Other visual areas (BAs 5, 18, 19, 20, 29, 30, 35, 36 and 37) also rank highly (e.g., in the top 20%) (Tables 1 and 2). On this evidence, visual perception was robustly in progress.[3]

<Insert Table 2 about here>

The next issue of interest is whether any regions with high-order duties showed increased activity on the *change block* while this visual processing was occurring. Using *mean standard density estimates per se* is appropriate for examining visual processing of the situation because participants were clearly fixating the displays, but high-order region activity need *not* be linked to the situation: participants may have been thinking of unrelated matters. To ensure that this activity was associated with the *change block* content, the *percentage increase* in the *standardised current density estimates* on this block relative to those on the *pre-change block* was calculated. This reflects the extent to which a region had engaged or "fired up" on the *change block* and locks the high-order region activity to loss of SA. To further ensure that only the most reactive regions were identified, a criterion of *at least 50% increase in activity* was applied.

In these terms, there was clear evidence of increased arousal in regions previously linked to high-order cognitive activity under uncertainty or error (see Table 1 for references)[3]: frontal BAs 6, 8, 9, 10, 11, 44, 45, 46, 47; anterior/posterior cingulate BAs 24, 31, 32, 33 and parietal BAs 7, 39, 40 (Table 3) [4]. There were individual profiles of response, but all participants showed increased activity in some of these high-order areas. If the mean *percentage increase* for all such areas is calculated for each participant, these scores significantly exceed the criterion of 50%: t (14) = 7.327, p <.001, d = 1.89 (mean 131.1, SD 42.9). These data thus confirm rapid and robust arousal of regions associated with high-end duties during this early processing interval during loss of SA. Of additional interest, there was also increased activity in regions for declarative memory (Hippocampus, BAs 21, 23, 27, 28, 34, 38) and affective arousal (BAs 13 and 25) (see Table 1b and 1c respectively for references).

<Insert Table 3 about here>

As noted, this arousal of high-order regions occurred when there was also vigorous activity in visual regions. For example, for the 12 participants with BA17 amongst their most active regions (consistent with active *primary* visual processing), there was concurrent arousal of regions with high-order duties (see all participants *except* 3, 11, 15 in Tables 2 and 3). See Figure 3 for a graphic example for one participant of co-activity in both frontal and visual areas at 150msec on the *change block*.

<Insert Figure 3 about here>

CONCLUSIONS EXPERIMENT 1

The important aspect of these results is that during loss of SA, there was rapid and robust engagement of brain regions associated with high-level cognitive processing while there was also active perceptual processing in Primary Visual Cortex (BA17) and associated visual regions. Even for Participants with BA17 amongst their most vigorous regions, there was evidence of engagement of areas with high-order functions. There was also strong evidence of arousal of regions linked to declarative and working memory with the loss of SA. High-level cognitive and memory operations may thus have been quickly engaged while level 1 visual-perceptual processing was in progress. Of additional interest was the arousal of areas linked to affective processing, consistent with emotional response to the loss of SA.

Such early co-activity of high- and low-order regions is not direct evidence of their interaction, but may provide a potential basis for it and is consistent with accounts of SA (Durso& Gronlund, 1999; Endsley, 2013) and neuroscience evidence (Rauss et al., 2011) indicating top-down influence on perceptual response. This experiment has clearly confirmed that during loss of SA, there may be rapid arousal of brain areas which contribute to high-order cognitive processing. The next experiment assesses whether this is even more likely in a task with more associations with natural situations.

EXPERIMENT 2: “URBAN THREAT” DETECTION EXPERIMENT

This experiment is similar to Experiment 1 in methods and analysis, except that more "natural" stimuli are used, with participants having to decide if a "terrorist threat" is present in photographs of urban scenes (e.g., an underground carriage). The main aim is again to determine if during loss of SA, brain regions with high-order duties are engaged during active perceptual (visual) processing. This task with more real-world content could produce even more extensive engagement of cognitive activity based on prior memory of a similar situation. The target information is whether a person in the scene has a bag or not. It should be stressed that this is not simply a perceptual "bag-spotting" task, but requires cognitive integration of a range of information to identify the correct target, consistent with level 2 SA. Although feedback is given as to correctness of response, no specific cues are provided and participants could focus on irrelevant attributes (ethnicity, age, etc.). Indeed many participants found the task challenging (see below).

METHOD

Participants. Initially 17 right-handed university students with no known neurological disorder completed the task (different sample to that in Experiment 1), but only 10 met the criterion for SA and were included in the final sample.

Design. The design was within-participant (participants doing both phases).

Apparatus and stimuli. Each display showed a colour photograph of a person in a natural urban scene (from open-access sources) (e.g., city streets). For Phase 1, the target feature defining the "threat" in each scene was whether a person had a bag of some kind (more complex categories were piloted, but participants failed to identify these). For Phase 2, the target category was whether the person was *not* carrying a bag.

The EEG apparatus was the same as for Experiment 1.

Procedure. The task involved the same basic structure as for Experiment 1: a series of 114 images were presented on a PC monitor via *E-prime* software, with 10 practice trials followed by 52 images for Phase 1 and the same 52 for Phase 2 (random image order in each Phase). Participants were instructed to act in the role of monitoring incoming images from surveillance cameras in the context of a possible terrorist threat to an urban environment and to identify whether or not the main subject of the picture constituted a "threat". Each image was followed by a probe question: *"The person in this slide represents a potential threat. T/F?"*. Each image remained on the screen until the participant made a response. Feedback on correctness of the response was then presented on-screen. To increase cognitive demand and "reality", a 'count' of lives saved/lost by the participant's responses (due to identifying or not identifying the threat) was also displayed, based purely on reaction time with faster responses losing fewer lives. Following the practice trials, the main trials were presented, without pause between Phase 1 and 2. Participants were then debriefed.

QASA was again used to provide SA (Knowledge) and Bias scores. During the task, brain activity was recorded with the EEG apparatus, using the same procedures for application of the net, acquisition and initial processing of the data and source estimation as for Experiment 1. The initial analysis of EEG data focussed on the 150-to-160msec post-stimulus interval on each trial as for Experiment 1. (See Experiment 1: Method for full details.) Additionally however for this experiment, further examination of the data at 100 - 110msec was conducted for reasons explained below.

RESULTS

QASA results: Six participants did not meet criterion SA ≥70 on the *pre-change block* and another P did not lose SA on the *change block*, so their data were not included for analysis. The remaining 10 participants showed a mean SA score of 96.21 (SD 3.13) on the *pre-change block*, with Bias scores ranging from -100 to +100. Their SA scores declined to a mean of 64.79 (SD 35.20) on the *change block* at the start of Phase 2, with this being a significant drop from the *pre-change block*: t (9) = 2.842, p =.019, d = 1.64, confirming an overall loss of SA. The decline in SA was accompanied by positive Bias shift for 6 participants, negative shift for 3 participants and no change for one participant, with the *percentage shift* (disregarding direction) being significant compared to no-change (0%): t (9) = 7.844, p <.001, d = 2.48. Thus the 10 participants demonstrated significant loss of SA and shift in Bias on the *change block.*

EEG activity during loss of SA on the Change Block Phase 2. Key areas of interest are again those for which prior evidence indicates roles in vision and cognition respectively (see Table 1).The first question is whether there is active visual perception on the *change block*. As for Experiment 1, all regions were ranked by the mean of their *standardised current density estimates* on the *change block*.[2] Primary visual cortex (BA17) was amongst the most active regions: for example, being amongst the top 20% for all 10 participants. Other higher-order visual perception areas (BAs 5, 18, 19, 20, 30, 35, 36 and 37) were also well-represented in the top 20% and almost identical to the inventory for Experiment1[3]. (See Tables 1 and 4). Notably, the mean *ranks* for these top 20% visual areas did not differ from those for Experiment 1: t (23) =. 940, p = .357, d = .37. (Experiment 1 mean rank: 8.6, SD 2.2; Experiment 2 mean rank: 9.6, SD 3.2). These data reflect vigorous activity in visual processing regions, comparable to that in Experiment 1.

<Insert Table 4 about here>

The next question is whether there was concomitant arousal of areas with high-order duties. As for Experiment 1, to ensure that this activity was associated with the current situation, *percentage increase* in the activity scores on the *change block* was again calculated and a criterion of ≥50% increase in activity was applied to reveal only strongly reactive regions. There were individual differences, but over the sample, the most reactive areas were almost identical to those in Experiment 1. Of most interest was the marked increase in activity in key areas for high-level cognition under uncertainty (frontal BAs 6, 8, 9, 10, 11, 44, 45, 46, 47; anterior cingulate BAs 24, 32, 33; posterior cingulate BA31; parietal BAs 7, 39, 40) (see Table 5 and Table 1 for references.) If the mean *percentage increase* for all such areas is calculated for each participant, these scores significantly exceed the criterion of 50%: t (9) = 3.98, $p < .003$, $d = 1.26$ (mean 132.2, SD 65.4). These scores are equivalent to those in Experiment 1: t (23) <1, p=.96, $d = .02$, reflecting comparably rapid and robust involvement of these high-order regions with the loss of SA. As for Experiment 1, this high-order region arousal was concurrent with activity in primary visual cortex (BA17) for all 10 Participants (see Tables 4 and 5).

<Insert Table 5 about here>

Of additional interest, there was also arousal of regions for declarative memory (Hippocampus, BAs 21, 23, 27, 28, 34, 38) and emotional/affective response (BA 13, 25) (see Table 1b and c).

Additional EEG Analyses at 100msec. The engagement of regions linked to high-level cognitive functions was thus remarkably rapid, but it is of interest to determine whether such arousal is evident at an even earlier interval. To this end, the EEG records for the 10 participants in this experiment were re-analysed at 100-110msec from stimulus onset in the same manner as for the 150-160msec data, to provide mean estimates of activity (*standardised current density*) across all Brodmann Areas and the Hippocampus on the *change block*. Regions of interest were again those previously implicated in visual perception and high-order cognition (Table 1).

The areas were ranked by their mean *standardised current density estimates*. There was strong activity in visual regions –for example, with BA17 and other visual regions strongly represented amongst the top 20% (see Table 6). The mean rankings (mean 9.6, SD 1.9) do not differ from those at the 150msec interval: t (9) = .008, p =.994, d = .003, with an identical overall inventory of regions, reflecting similar engagement of visual regions at both intervals.

<Insert Table 6 about here>

Areas with high-order duties also showed increased activity on the *change block* at this 100msec interval (*percentage increase* from the *pre-change block*, calculated as before). Again adopting a conservative criterion of ≥50% increase in activity, all participants showed at least four such areas (see Table 7). The mean *percentage increase* across these areas for each participant again exceeds the criterion of 50%: t (9) = 2.852, p = .019, d = 0.90 (mean: 154.67, SD 116.05), indicating vigorous arousal.

<Insert Table 7 about here>

CONCLUSIONS EXPERIMENT 2

The results again testify to early engagement of cortical regions associated with high-order cognitive functions under uncertainty even at 100msec. The increased arousal of these regions is tied to the loss of SA on the *change block* and is concurrent with active processing in visual perception regions. There is also evidence of engagement of regions for working and declarative memory and emotional arousal. These results closely resemble and extend the findings of Experiment 1 to include content relevant to natural situations.

OVERALL DISCUSSION

In both experiments, loss of SA was accompanied by concurrent engagement of visual regions and high-order frontal, cingulate and parietal regions associated with cognition under uncertain conditions. There was also strong arousal in regions associated with memory functions indicating rapid memory operations during loss of SA. Although the precise patterns of brain response varied with individuals and may vary across situations, both experiments show comparably rapid and early co-activity of visual and higher-order regions for both "abstract" and more real-world content. The evidence of such co-activity at 100msec is remarkable, given that decision-related perceptual processing can require 250msec (van Rullen &Thorpe, 2001) and reporting of visual input 400msec (Jolij et al., 2011).

Importantly, the methods employed ensure that this brain activity is directly linked to loss of SA. The identified high-order regions have been formerly linked to cognition under uncertainty (Table 1) but this constitutes the first evidence of their association with measured loss of SA and may offer valuable insights in this regard. For example, for many participants, with loss of SA, orbitofrontal cortex (BA11) was strongly activated. This area receives rapid perceptual and affective input, contributing to an "early warning system" about uncertain or affectively-charged contexts (Kveraga, Ghuman,& Bar, 2007; Table 1), and may have broadcast early top-down signals about the loss of SA.

It must be stressed that co-activity of high-order and visual regions is not evidence of their interaction. Nevertheless it offers more fertile conditions for this than would a linear processing trajectory where active perception diminishes before high-order areas are engaged. The current evidence is thus critical in confirming the *opportunity* for early interaction of high-order and visual-perceptual regions, reflecting potential conditions for rapid top-down influence on perception during loss of SA.

The timing and mechanisms of any top-down influence on perception have yet to be decided (e.g., Fu et al., 2012; Rauss et al., 2012), but re-entrant feedback from high-order brain regions can influence visual processing (Bar, 2003; Furmanski, et al., 2004; Poghosyan & Ioannides, 2008; Rauss, et al., 2011, etc.). Top-down signals are beneficial in "Recognition-Primed Decision-Making" (Klein et al., 2010), but if flawed or irrelevant, may distort perception. In a natural situation resembling that in Experiment 2, top-down processing (expectation, fear) could cause premature judgment that someone's bag contained an explosive device, terminating visual scrutiny/analysis that may reveal the bag to be empty. Many cases of loss of SA may be explained by such top-down modulation of perceptual processing. As noted, the Mt Erebus, Storm King Mountain and Eastern Airlines tragedies could conceivably have involved such processing scenarios.

These results contribute to theoretical understanding of SA. Of most importance they support incorporation of top-down influences (expectation, memory, etc.) in models of SA at level 1 (Durso & Gronlund, 1999; Endsley, 2013). As noted, this may be profoundly important in explaining cases of loss of SA. Secondly, the results coalesce theoretical approaches and endorse neuroergonomic methods to studying SA (Parasuraman & Wilson, 2008) by demonstrating correspondence between behavioural *product* (SA as knowledge) and *process* (corresponding brain activity) and so further affirming that despite review (Dekker & Hollnagel, 2004), the construct of SA has resonance in brain processes as well as behaviour.

SA models may also benefit from the evidence here of activity in ventral ACC (BA25) and the insula, possibly reflecting affective arousal (see Table1). Some individuals may react to loss of SA with negative affect, causing perceptual tunnelling (Gable & Harmon-Jones, 2010) and hampering reattainment of SA (Causse et al., 2013a). This may link to the Bias shifts accompanying loss of SA. Most participants showed more conservative bias with loss of SA (tunnelling) although others showed more liberal bias (less exacting), with potential implications for regaining lost SA. It may be important to include emotional response and bias in models and assessments of SA.

Individual differences were apparent in the location and number of active brain regions, possibly reflecting different strategies for recouping level 2 SA. Since any such strategy involves some high-order brain activity, this did not detract from the main aim to observe concurrent engagement of high- and low-order regions. Nevertheless, dispersion of brain activity discriminates novices from experts (Peres, et al., 2000) and may offer a useful focus for further study.

Another issue of interest is that the active areas were often lateralised. Asymmetry of brain processes linked to SA may be a valuable focus for further research. For example, right hemisphere dominance occurs in vigilance for simple (but not complex) tasks (Helton, Warm, Tripp, Matthews, Parasuraman, & Hancock, 2010) with possible ramifications in operational contexts where location of items in the visual field is critical.

The current results point to the importance of monitoring top-down factors during real-world operations. Even highly trained professionals may be susceptible to perceptual error due to faulty top-down expectation. On the fireground for example, well-trained firefighters may overlook a potential hazard such as a gas cylinder if not anticipating its presence (Catherwood et al., 2012). It is beyond the scope of the current paper to advocate specific strategies for improving operational risk due to such faulty top-down influences. Augmented cognition (AugCog) systems can, however, support perception in challenging situations such as the fireground (Wilson & Wright, 2007). Although currently a distant possibility, the real-time measurement of bias (using EEG or functional near infra-red spectroscopy – fNIRS) could provide a valuable input into an augmented cognition system to give feedback to operators concerning their information-handling bias. The amount and type of information provided to the user could also be adapted as part of an augmented cognition system able to track user bias.

Nevertheless, even if feasible, such a system should be used cautiously. There is no guarantee that perceptual information delivered by AugCog systems will necessarily be employed by potential users. Such information may also be vulnerable to top-down effects (expectations, memories, emotional arousal, etc.) producing perceptual distortions or oversights: availability of information is not sufficient to ensure accurate perception. The current data show that individuals may vary in the criterion or bias towards employing the available information. Loss of SA here was accompanied by shifts in bias- towards either rejecting or accepting the available information, respectively associated with “miss” or “false alarm” errors. Top-down influences may induce such bias, producing failure to make optimal use of available information. It may be feasible to adapt the amount of information presented and the method for presenting it depending on the operator’s bias, but the top-down influences discussed above may still affect how that information is used.

Another possibility is to develop training routines that promote self-monitoring of such biases and of the nexus between top-down expectations and current perception. Such self-checks could possibly employ a tool such as QASA to provide feedback on bias tendencies. Whatever the adopted strategy however, it should clearly acknowledge the potential for rapid high-end influence on visual perception of the situation.

In sum, the current investigation reveals rapid co-engagement of visual and high-order regions during loss of SA. While not direct evidence of interaction of these regions, this co-activity indicates a basis for top-down effects on perception during loss of SA that may explain why highly-skilled professionals fly aircraft into visible mountains or overlook perceptible wind shifts while fighting wildfires.

Footnotes

[1]QASA was originally developed as QUASA^{TM} (Edgar & Edgar, 2007) based on nominally non-parametric signal detection measures, but has also been implemented using parametric measures. The tool here uses the original nominally *non-parametric* approach and so is described as QASA to clarify the distinction in methods.

[2]Standardised current density estimates do not provide measures of absolute activation (Pascual-Marqui, 2002) so the analyses here employ within-participant rankings and percentage changes.

[3]The regions of high activity occurred in either left or right Brodmann Areas, but both left and right regions are represented over the sample in both experiments.

[4] BA8 was once considered to house the human frontal eye fields but these are now considered to be in BA6 (Brignani et al., 2007; Grosbras et al., 1999; Rosano et al., 2002), but both areas have been linked to task-reversal (see Table 1 for references).

KEY POINTS

- 128-channel EEG data and estimates of Situation Awareness (SA) and Bias using QASA were obtained during enforced loss of SA in one task requiring identification of a target pattern (N=15) and in another task of "threat" in urban scenes (N=10).

- Participant brain activity was examined 150msec post-stimulus-onset in both tasks and 100msec in the second task and sources of activity identified with sLORETA.

- There was significant loss of SA and Bias shifts, with associated activity in brain regions for visual perception concurrent with arousal of cortical regions for cognitive operations under ambivalent, task-switching conditions (e.g., BA7, 9, 11, 46, 47).

- The strong co-activity in visual and high-order brain regions may reflect a basis for rapid top-down influence (expectation, memory) on perception (level 1 SA).

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FIGURE TITLES/CAPTIONS

Figure 1. Example of displays in Experiment 1 (target= 3 lines + red)

Figure 2. Example of the Electrical Geodesics Incorporated 128-channel EEG GeoDesic Sensor Nets used in both Experiment 1 and 2

Figure 3. Experiment 1: GeoSource representation for one Participant of brain activity during loss of SA on the "change block" at 150msec after stimulus onset averaged across trials: Peak activity (crosshairs) is in LBA11 (left orbitofrontal region) but with co-activity in other areas including RBA17 (V1). These displays consist of estimated source data shown as dipoles overlaid on 3D MRI sagittal, coronal and axial views of the "typical" Montreal Neurological Institute brain.

FIGURES

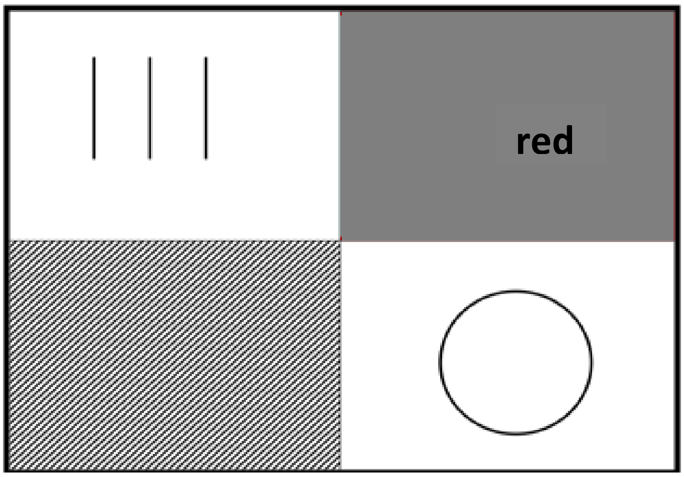

Figure 1

Figure 2

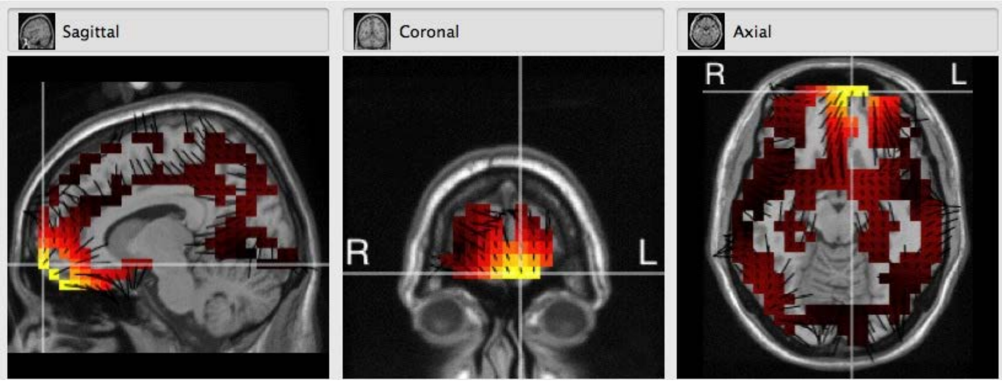

Figure 3

Table 1: References for key Brodmann Areas active in both Tasks and *some* associated *key* functions *relevant to current tasks*[1]

(a.) <u>PRIMARY AND HIGHER-LEVEL VISUAL PROCESSING: (LEVEL 1 SA):</u>

- **BA 05 (with BA07, superior parietal lobule)** : spatial perception and imagery (Thompson et al., 2009; Wenger et al., 2012)
- **BA17 primary visual/striate cortex (V1) :** primary visual processing(Amunts, Malikovic, Mohlberg et al., 2000)
- **BA18 & BA19 extra-striate occipital cortex (precuneus, cuneus, lingual gyrus, lateral occipital gyrus**): colour, shape, motion perception; contour integration (Tanskanen et al., 2009; Thompson et al., 2009); figural/spatial reasoning (Goel et al., 1998)
- **BA 20 infero-temporal cortex:** high-level visual processing and memory including for colour; visual categorization (Afifi & Bergman, 2005; Visser et al., 2010)
- **BA29 and BA30 part of retrosplenial cortex**: episodic memory (Maguire 2001), but also: high-level visual scene integration (invariant representation) (Bar & Aminoff, 2003; Henderson et al., 2008; Park & Chun, 2009; Vann et al., 2009)
- **BA35 & BA36 perirhinal cortex:** object recognition but also: complex visual feature binding (colour, etc.) and discrimination; figure-ground perception (Barense, et al., 2011; Bellgowan, et al., 2009; Bussey et al., 2005; Lee et al., 2005; Murray & Richmond, 2001; Staresina & Davachi, 2008)
- **BA 37 infero- temporal region:** colour / shape binding, attention, memory & judgments (Kastner & Ungerleider, 2000; Soie et al., 2009)

(b.) <u>WORKING/DECLARATIVE MEMORY (ALL LEVELS SA):</u>

- **BA 21 middle temporal gyrus**: verbal/semantic working memory (Schivde & Thompson-Schill, 2004)
- **BA 23: posterior cingulate cortex**: episodic memory (Sugiura et al., 2005; Salimpoor et al., 2009)
- **BA 28 & BA 34**: **part of entorhinal cortex:** declarative/episodic memory system; spatial-object memory (Bellgowan et al., 2009; Jeffery, 2007; Preston & Gabrieli, 2002; Schott et al., 2011)
- **Hippocampus and BA 27 in hippocampal formation:** working memory ; memory consolidation-binding (Axmacher et al., 2010; Finke et al., 2008; Hassabis et al., 2009; Lee et al., 2005; Morgan et al., 2011; Piekema et al., 2006; Staresina & Davachi, 2009; Vann & Albasser, 2011; Wixted & Squire, 2010)
- **BA 38: temporal pole:** declarative memory ; binds emotion & perception; insight, passive conceptualisation (Blaizot et al.,2010; Kröger et al., 2012; Olson et al., 2007; Simmons & Martin, 2009)

(c.) <u>AFFECTIVE/EMOTIONAL ROLES (ALL LEVELS SA):</u>

- **BA13 anterior insula** : Interoception (Cauda et al., 2011) reward-related / risky/ aversive decision-making or learning (Causse et al., 2013a; Craig, 2009; Wittmann et al., 2010)
- **BA 25: anterior cingulate cortex:** "affective" division of ACC (Bush, Luu & Posner,2000; Luu & Posner, 2003; Paus 2001)

(d.) <u>HIGH-ORDER COGNITION: TASK INTEGRATION/APPRAISAL/HYPOTHESIS-TESTING/ SWITCHING (LEVELS 2 AND 3 SA):</u>

- **BA 06 Supplementary Motor Area (SMA:** criterion-, task- and rule –switching under uncertainty; response conflict monitoring (Dove, 2000; Crone et al., 2006; Hanakawa et al., 2002; Miller et al., 2001; Woodward et al., 2008;); Human FEF (Brignani et al., 2007; Rosano et al., 2002)
- **BA07 superior parietal lobule/precuneus:** task-switching ; spatial cognition (Brass & von Cramon, 2004; Crone et al., 2006; Curtis et al., 2004; Rushworth et al., 2002; Thompson et al., 2009)
- **BA8 pre-SMA (pre-supplementary motor area):** decisions under uncertainty/conflict; visuo-spatial working memory (Bhanji et al., 2010;Volz et al., 2004; Woodward et al., 2008)**;** formerly thought to be FEF (but now these considered to be in BA6)
- **BA 9 dorsolateral PFC:** use/switch of complex rules; hypothesis-testing; ambivalence, low confidence, negative feedback; attention;working memory for new goals (Bunge & Zelazo, 2006; Burgess et al., 2007; Causse et al., 2013b; Crone et al., 2006; Fleck et al., 2006; Jung et al., 2008; Miller, 2001; Schnider et al., 2005; Zanolie et al., 2008)
- **BA10 frontal polar area:** mediates stimulus-oriented vs independent attention (Burgess et al., 2007; Okuda, Gilbert, Burgess, Frith, Simons, 2011); other functions as above for BA09
- **BA 11 orbitofrontal cortex:** monitors expected S-R contingencies especially if rewarding/ evaluative/ affective aspects & ambivalent conditions and if need to reverse S-R associations (Bunge 2006; Jung et al., 2008; Kringelbach & Rolls, 2004;Kveraga, Ghuman, & Bar, 2007; Öngur & Price, 2000; Zald & Rauch, 2006)
- **BA 24, BA32 and BA33: Anterior Cingulate Cortex**: responds to violations of S-R associations & uncertainty; conflict and error detection (Botvinik, Cohen & Carter, 2004; Bush et al., 2000; Deppe et al., 2005; Kerns et al., 2004; Paus, 2001; Miller et al., 2001)
- **BA 31: Posterior Cingulate Cortex:** task-switching involving colour (Dove at al., 2000)
- **BA 39 (angular gyrus):** Language but also: arithmetical cognition; object- location working memory (Sestieri et al., 2011; Shah et al., 2012)
- **BA40 (supramarginal gyrus** – with BA39 = Inferior Parietal Lobule): visuo-spatial cognition; divergent problem-solving (Arsalidou & Taylor, 2011;Uddin et al., 2010; Shah et al., 2011; Silk et al., 2010)
- **BA 44-45: Broca's Area**[2] verbal working memory but also hypothesis-testing, task-switching/ rule-based choices (Bhanji et al., 2010; Dove et al., 2000; Elliott & Dolan, 1998)
- **BA46 (part of dorsolateral PFC):** rule-switching especially if low confidence; visuo-spatial cognition (Bunge & Zelazo, 2006; Crone et al., 2006; Fleck et al., 2006)
- **BA47: orbitofrontal/ventrolateral frontal cortex:** switching tasks and rules; implications of negative events for future actions; contextual relevance of emotion in decision-making (Beer et al., 2006; Elliott, Dolan, & Frith, 2000; Kringelbach & Rolls, 2004; Zanolie et al., 2008)

[1] ***This is meant to be a general guide to SOME key roles for the Brodmann Areas which can have numerous functions and are often part of larger networks. Any area active in cognition under uncertainty has been classified here as "high-order".*** [2]***BA44 and 45 (Broca's Area) are associated with speech function but also with verbal rehearsal and working memory and hypothesis-testing.***

Table 2

EXPERIMENT 1: WISCONSIN CATEGORY TASK:

Brodmann Areas associated with Visual Perception in the top 20% of ranked Brodmann areas for mean activity on *Change Block* at 150msec

Participant												
P1	**L17**	**R17**	**L35**	**R35**	**R18**	**R30**	**L36**	**L18**	**L30**	**R36**	**R37**	**--**
rank in top 20%	**1**	**2**	**3**	**6**	**7**	**8**	**9**	**10**	**12**	**13**	**18**	
P2	**R37**	**R18**	**R20**	**R36**	**R30**	**R17**	**R35**	**L17**	**R19**	**L36**	**L20**	**L35**
rank	**1**	**2**	**3**	**5**	**6**	**7**	**8**	**9**	**11**	**14**	**15**	**16**
P3	**R35**	**--**										
rank	**7**											
P4	**L17**	**R17**	**R18**	**L18**	**L35**	**R35**	**L36**	**R36**	**L30**	**--**		
rank	**1**	**2**	**3**	**4**	**5**	**6**	**8**	**12**	**13**			
P5	**L17**	**L36**	**L35**	**R17**	**R18**	**L18**	**L37**	**L20**	**L30**	**R30**	**--**	
rank	**1**	**2**	**3**	**4**	**7**	**8**	**9**	**11**	**12**	**17**		
P6	**L17**	**R17**	**R5**	**L36**	**L35**	**R35**	**--**					
rank	**3**	**5**	**13**	**15**	**16**	**17**						
P7	**R35**	**R36**	**R20**	**R18**	**R30**	**L17**	**R37**	**L36**	**R17**	**L35**	**--**	
rank	**2**	**3**	**9**	**10**	**11**	**12**	**13**	**14**	**16**	**18**		
P8	**L36**	**L35**	**R17**	**L20**	**R36**	**R30**	**R35**	**R18**	**--**			
rank	**4**	**5**	**8**	**9**	**12**	**14**	**17**	**18**				
P9	**L17**	**R20**	**R35**	**R17**	**R36**	**L18**	**L30**	**--**				
rank	**3**	**4**	**6**	**7**	**8**	**13**	**17**					
P10	**L17**	**R17**	**R20**	**R18**	**L18**	**R30**	**R37**	**L30**	**--**			
rank	**1**	**2**	**4**	**5**	**6**	**10**	**11**	**15**				
P11	**R35**	**L35**	**L36**	**R36**	**R30**	**--**						
rank	**1**	**6**	**11**	**12**	**15**							
P12	**R17**	**L35**	**L36**	**R18**	**R35**	**R36**	**L30**	**L17**	**--**			
rank	**1**	**2**	**3**	**9**	**12**	**15**	**16**	**17**				
P13	**R35**	**R36**	**R20**	**R37**	**R30**	**L17**	**R17**	**L35**	**R18**	**L36**	**--**	
rank	**1**	**2**	**7**	**9**	**10**	**12**	**13**	**15**	**16**	**18**		
P14	**R17**	**L17**	**R18**	**R30**	**L18**	**L30**	**R35**	**R19**	**L36**	**R36**	**R29**	**--**
rank	**1**	**2**	**3**	**4**	**5**	**7**	**11**	**14**	**15**	**16**	**17**	
P15	**R35**	**R36**	**R20**	**R37**	**--**							
rank	**6**	**8**	**15**	**18**								

L= left Brodmann Area R= right Brodmann Area -- no further regions meeting the criterion

Table 3

EXPERIMENT 1: WISCONSIN CATEGORY TASK: Brodmann Areas associated with "high-order" cognition that showed at least 50% *increase in activity from the pre-change block to the change block* (ranked from left by *percentage increase*)

Participant	most increase	➡											
P1	**R39**	**L40**	**R44**	**--**									
% increase	82.1	74.8	59.3	--									
P2	**R 46**	**L 08**	**L45**	**L06**	**R10**	**L44**	**R11**	**R40**	**L46**	**--**			
% increase	225.5	220.3	98.6	94.5	92.4	88.4	76.5	65.1	59.3	--			
P3	**L 10**	**L 44**	**L 09**	**L 11**	**L 45**	**R 33**	**L33**	**R32**	**R10**	**R7**	**L47**	**L32**	**L46**	**--**
% increase	173.8	160.5	159.6	148.1	147.9	129.4	124.4	117.3	98.1	91.3	84.9	74.6	59.2	--
P4	**R 09**	**L 09**	**L47**	**L06**	**L24**	**R46**	**L11**	**L32**	**--**					
% increase	160.0	136.3	89.9	77.1	72.2	69.7	59.8	54.4	--					
P5	**L06**	**R 47**	**R 07**	**R44**	**--**									
% increase	378.9	204.9	166.1	82.2	--									
P6	**R 07**	**R 31**	**L 31**	**R 39**	**L 07**	**R44**	**L24**	**R24**	**R33**	**R45**	**--**			
% increase	579.2	434.1	204.1	203.1	181.5	112.7	102.5	96.5	57.2	56.5	--			
P7	**R39**	**R40**	**R06**	**--**										
% increase	89.7	88.5	66.2	--										
P8	**L 09**	**L 10**	**L 11**	**R 44**	**L 47**	**L40**	**L06**	**R06**	**--**					
% increase	288.5	263.1	162.7	126.2	121.4	91.5	71.7	64.4	--					
P9	**R 44**	**R 47**	**R32**	**L32**	**R33**	**R45**	**L10**	**R11**	**L06**	**L33**	**L11**	**L24**	**L47**	**--**
% increase	251.8	241.7	141.5	135.5	125.5	140.4	104.1	99.1	97.0	90.4	75.6	66.2	54.0	--
P10	**R 31**	**L 31**	**R 39**	**L24**	**R24**	**R11**	**R47**	**R33**	**L33**	**R07**	**L08**	**L07**	**L11**	**R06**
% increase	464.6	395.3	319.1	279.7	253.6	130.9	127.7	115.8	113.0	91.5	90.4	73.1	69.4	56.2
P11	**R 40**	**L 11**	**L 07**	**R 11**	**L44**	**--**								
% increase	169.2	165.6	108.1	100.1	71.0	--								
P12	**R40**	**R47**	**L33**	**L24**	**L32**	**R33**	**R11**	**L09**	**--**					
% increase	166.2	152.3	118.2	93.4	88.7	64.5	53.4	50.7	--					
P13	**R 45**	**R 44**	**R47**	**R11**	**R09**	**R33**	**L44**	**R06**	**--**					
% increase	553.0	235.9	144.2	127.6	126.2	66.4	62.2	61.2	--					
P14	**L 39**	**R11**	**L 11**	**L 47**	**R40**	**L07**	**R07**	**R09**	**--**					
% increase	198.3	142.1	131.9	113.5	88.5	70.2	67.2	63.8	--					
P15	**R 39**	**L33**	**R33**	**L08**	**L 24**	**R24**	**L32**	**--**						
% increase	171.8	159.3	150.3	118.3	111.5	85.2	63.1	--						

(L= left and R= right Brodmann Area) (-- no further regions meeting the criterion) (BAs 1,2,3,4,41,42,43: primary somatosensory, motor, auditory BAs excluded: not relevant to task)

Table 4

EXPERIMENT 2: URBAN THREAT TASK:

Brodmann Areas associated with Visual Perception in the top 20% of ranked Brodmann areas for mean activity on *Change Block* at 150msec

Participants:									
P1	**L20**	**L17**	**L36**	**L35**	**R35**	**R5**	**R19**	**L5**	**L18**
rank	**3**	**4**	**5**	**6**	**8**	**9**	**11**	**12**	**18**
P2	**R5**	**L5**	**R20**	**R36**	**R17**	**R35**	**R18**	**R19**	**--**
rank	**3**	**4**	**5**	**8**	**9**	**10**	**11**	**14**	**--**
P3	**L17**	**R17**	**L18**	**R19**	**R20**	**R35**	**R36**	**R30**	**--**
rank	**1**	**2**	**4**	**7**	**8**	**9**	**14**	**15**	**--**
P4	**R36**	**R35**	**R20**	**L35**	**L17**	**L36**	**--**		
rank	**9**	**10**	**13**	**16**	**17**	**18**	**--**		
P5	**R35**	**R36**	**R17**	**R13**	**--**				
rank	**5**	**9**	**13**	**14**	**--**				
P6	**L35**	**L36**	**L37**	**L20**	**L30**	**L17**	**R17**	**L18**	**R37**
rank	**1**	**2**	**6**	**8**	**9**	**11**	**13**	**14**	**18**
P7	**R35**	**R36**	**R30**	**R17**	**R18**	**R37**	**L35**	**L36**	**--**
rank	**1**	**3**	**6**	**7**	**8**	**10**	**15**	**17**	**--**
P8	**R17**	**L17**	**L30**	**R18**	**L35**	**L36**	**L18**	**L37**	**--**
rank	**1**	**2**	**4**	**5**	**6**	**7**	**8**	**9**	**--**
P9	**R35**	**R36**	**L17**	**--**					
rank	**15**	**16**	**18**	**--**					
P10	**R5**	**L5**	**L30**	**R17**	**--**	**--**			
rank	**2**	**6**	**15**	**16**	**--**	**--**			

L= left Brodmann Area; R = right Brodmann Area -- no further regions meeting the criterion

Table 5

EXPERIMENT 2: URBAN THREAT TASK: 150msec data: Brodmann Areas associated with "high-order" cognition that showed at least 50% *increase in activity from the pre-change block to the change block* (ranked from left by *percentage increase*)

P	most increase	→													
P1	**L46**	**R07**	**L07**	**R31**	**--**										
%	163.0	147.8	106.2	80.9	--										
P2	**L31**	**R32**	**R31**	**R24**	**R07**	**R33**	**L07**	**L24**	**R11**	**L32**	**R06**	**R44**	**R40**	**L33**	**R08**
%	124.7	123.0	112.6	87.8	87.4	83.0	81.2	78.9	78.5	77.1	75.9	71.3	66.7	65.3	52.5
P3	**R08**	**R07**	**L07**	**R31**	**L31**	**L39**	**--**								
%	185.2	150.3	146.4	127.3	94.5	78.3	--								
P4	**L11**	**R11**	**R06**	**L32**	**R32**	**L47**	**L33**	**R33**	**R10**	**L10**	**--**				
%	175.3	136.0	128.2	126.2	114.0	103.1	94.2	93.2	73.4	65.0	--				
P5	**R46**	**L09**	**R45**	**R09**	**L08**	**L44**	**R08**	**L46**	**--**	**--**					
%	676.7	317.9	286.9	285.2	254.4	223.3	182.9	170.1	--	--					
P6	**R09**	**R10**	**--**												
%	113.9	84.6	--												
P7	**L31**	**R06**	**L06**	**L39**	**R24**	**R31**	**L08**	**R09**	**L24**	**R40**	**R46**	**R32**	**R39**	**--**	
%	242.2	215.6	169.7	132.6	89.2	89.1	85.1	77.7	70.3	66.0	53.8	53.8	53.1	--	
P8	**L10**	**L31**	**L11**	**R06**	**L47**	**--**									
%	185.4	94.2	71.5	63.0	60.2	--									
P9	**L07**	**R31**	**L09**	**--**											
%	106.0	104.4	53.2	--											
P10	**L10**	**L46**	**L07**	**L08**	**R07**	**R24**	**L24**	**L11**	**--**						
%	536.2	223.9	219.2	117.3	114.1	107.4	92.4	50.9	--						

(L= left and R= right Brodmann Area) (-- no further regions meeting the criterion) (BAs 1,2,3,4,41,42,43: primary somatosensory, motor, auditory BAs excluded: not relevant to task)

Table 6

EXPERIMENT 2: URBAN THREAT TASK:

Brodmann Areas associated with Visual Perception in the top 20% of ranked Brodmann areas for mean activity on *Change Block* at 100msec

Participant											
P1	**R35**	**R36**	**L36**	**L35**	**L20**	**R20**	**L37**	**R17**	**R30**	**--**	
rank	**2**	**4**	**5**	**11**	**12**	**15**	**16**	**17**	**18**	**--**	
P2	**R20**	**R35**	**R36**	**L17**	**R5**	**L5**	**R17**	**R37**	**--**		
rank	**3**	**4**	**5**	**10**	**11**	**15**	**17**	**18**	**--**		
P3	**L17**	**L18**	**L30**	**R17**	**R35**	**R19**	**L37**	**R30**	**R36**	**L35**	**--**
rank	**1**	**2**	**3**	**5**	**6**	**13**	**14**	**15**	**16**	**18**	**--**
P4	**R17**	**L17**	**R18**	**R30**	**L35**	**R20**	**R35**	**--**			
rank	**1**	**7**	**8**	**12**	**15**	**16**	**17**	**--**			
P5	**R35**	**R37**	**R36**	**L35**	**L36**	**--**					
rank	**5**	**6**	**7**	**14**	**18**	**--**					
P6	**L35**	**R35**	**L36**	**R36**	**--**						
rank	**8**	**11**	**13**	**15**	**--**						
P7	**R35**	**R36**	**R30**	**R37**	**L30**	**L35**	**L17**	**R18**	**--**		
rank	**1**	**3**	**6**	**12**	**15**	**16**	**17**	**18**	**--**		
P8	**L17**	**R17**	**L30**	**L18**	**R35**	**L35**	**L36**	**R37**	**R19**	**R30**	**L19**
rank	**1**	**2**	**3**	**4**	**7**	**8**	**9**	**11**	**12**	**14**	**17**
P9	**R17**	**L17**	**L30**	**R30**	**L18**	**L19**	**R18**	**R35**	**--**		
rank	**1**	**5**	**6**	**8**	**9**	**10**	**12**	**16**	**--**		
P10	**L20**	**L36**	**L35**	**L37**	**--**						
rank	**1**	**4**	**5**	**12**	**--**						

L= left Brodmann Area; R = right Brodmann Area -- no further regions meeting the criterion

Table 7

EXPERIMENT 2: URBAN THREAT TASK: 100msec data: Brodmann Areas associated with "high-order" cognition that showed at least 50% *increase in activity from the pre-change block to the change block*)

(ranked from left by *percentage increase*)

p	most increase	→													
P1	**L40**	**R10**	**R46**	**L08**	**L46**	**L09**	**L33**	--							
%	140.1	96.5	86.4	81.5	79.0	78.3	54.2	--							
P2	**L10**	**L47**	**L45**	**L46**	**L44**	**R32**	**R10**	**L08**	**R47**	**R45**	**R44**	--			
%	294.5	223.6	222.9	161.7	160.9	149.7	122.8	74.7	69.6	68.3	60.7	--			
P3	**R33**	**R24**	**L31**	**R31**	**R07**	**L24**	**R11**	**R40**	--						
%	114.3	85.2	81.5	80.2	68.2	66.5	63.2	54.2	--						
P4	**L31**	**R39**	**R31**	**R11**	--										
%	222.2	93.7	85.8	57.0	--										
P5	**R46**	**L46**	**L45**	**L44**	**L09**	**R45**	**L08**	**R06**	**R08**	**R44**	**R39**	**R09**	**L47**	**R10**	**R47**
%	1446.1	998.3	788.1	716.3	526.4	491.9	433.3	353.5	351.3	240.9	208.4	184.6	152.6	144.0	59.1
P6	**R32**	**L33**	**L32**	**R33**	**R11**	**L11**	**L34**	**R34**	**R08**	--					
%	135.6	93.4	87.4	85.6	77.1	74.2	72.1	72.1	59.7	--					
P7	**L07**	**R07**	**L06**	**R40**	**L31**	**R24**	**L24**	**R32**	**R06**	**R09**	**R08**	**R31**	--		
%	318.8	187.8	169.7	132.0	128.7	90.3	86.2	85.1	72.5	66.9	61.9	51.6	--		
P8	**R32**	**L39**	**L32**	**L31**	**L07**	--									
%	344.8	118.0	78.0	59.5	51.8	--									
P9	**R08**	**R32**	**R09**	**R46**	**R44**	**L45**	**L32**	**R33**	**R24**	**L09**	**R06**	**L33**	**R40**	--	
%	276.3	240.4	212.6	171.8	140.9	135.6	129.5	107.0	73.7	71.0	68.5	65.0	54.9	--	
P10	**L46**	**L10**	**L45**	**R47**	**L47**	**R10**	**R46**	**R09**	**L44**	**L11**	**L39**	--			
%	442.1	395.5	284.5	199.0	117.9	109.6	99.7	92.0	90.5	67.9	61.0	--			

(L= left and R= right Brodmann Area) (-- no further regions meeting the criterion) (BAs 1,2,3,4,41,42,43: primary somatosensory, motor, auditory BAs excluded: not relevant to task)

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