

Dissociation between semantic representations for motion and action verbs: Evidence from patients with left hemisphere lesions

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Dissociation between semantic representations for motion and action verbs: Evidence from patients with left hemisphere lesions
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Abstract

This multiple single case study contrasted left hemisphere stroke patients (*N*=6) to healthy age-matched control participants (*N*=15) on their understanding of action (e.g., holding, clenching) and motion verbs (e.g. crumbling, flowing). The tasks required participants to correctly identify the matching verb or associated picture. Dissociations on action and motion verb content depending on lesion site were expected. As predicted for verbs containing an action and/or motion content, modified t-tests confirmed selective deficits in processing motion verbs in patients with lesions involving posterior parietal and lateral occipitotemporal cortex. In contrast, deficits in verbs describing motionless actions were found in patients with more anterior lesions sparing posterior parietal and lateral occipitotemporal cortex. These findings support the hypotheses that semantic representations for action and motion are behaviourally and neuro-anatomically dissociable. The findings clarify the differential and critical role of perceptual and motor regions in processing modality-specific semantic knowledge as opposed to a supportive but not necessary role. We contextualise these results within theories from both cognitive psychology and cognitive neuroscience that make claims over the role of sensory and motor information in semantic representation.

Keywords: neuropsychology; left hemisphere; lateral occipitotemporal cortex; affordances; embodied cognition; semantic representation; aphasia.

1. Introduction

The motor system is primarily engaged for the execution of actions, but has also been shown to be engaged when familiar actions are observed (e.g., Calvo-Merino et al., 2006), imagined (e.g. Decety, 1996), or even read about (Beilock et al, 2008). For example, reading a sentence describing action primes bodily movements matching the referential content (e.g., Glenberg & Kaschak, 2002). Such evidence is frequently taken to support the notion that bodily and action representations are routinely recruited to derive meaning from language (Gallese & Lakoff, 2005; Fischer & Zwaan, 2008). Research over the past decade has demonstrated that language describing familiar actions results in activation of motor systems (e.g. Kemmerer et al., 2008; Pulvermüller, 2005). However, despite the broad and high-profile theoretical claims made in the literature about language understanding and sensorimotor systems, the necessity of such recruitment has not been firmly established. For example, the effects found might be merely epiphenomenal or the case may be that "sensory and motor information plays, at best, a supportive but not necessary role in representing concepts" (Mahon & Caramazza, 2008, p. 67). This debate has led others to propose a middle ground - that relying on both 'embodied' and 'symbolic' mechanisms provides language users with richer and more fault-tolerant representations (Taylor & Zwaan, 2012; Dove, 2009; Andrews, Vigliocco & Vinson, 2009). What would clarify this debate however, is evidence to suggest that 'embodied' and 'symbolic' representations dissociate, and also that varying "perceptual" brain regions may be implicated even within a semantic category. Indeed verbs do not always refer to concrete, dynamic actions; verbs can also refer to events involving movement, mental states, and can state a change. A raindrop might fall to earth and a flower might wilt, resulting in visual motion, but we cannot directly realize such events with our bodies as we might when we hit (a concrete, dynamic action; as described in Table 1 labelled +Action/+Motion verbs) or hold an object (a motionless action; as described in Table 1 labelled as the +Action/-Motion Category in our research design).

Brain imaging and behavioural studies alone provide limited information about the relationship between cognitive processes: motor system activation may be a consequence or correlate of comprehension, not a cause (see e.g., David & Senior, 2000 for a further debate). Additional persuasive evidence comes from patients and participants with lesions affecting the brain's motor system who show a specific impairment for action knowledge; a trend that has been demonstrated for Motor Neurone Disease, Parkinson's Disease, and stroke (Kalenine et al., 2010; Bak et al., 2006; Boulenger et al., 2007; Arévalo et al., 2007; Neiniger & Pulvermüller, 2003). While analogous evidence from healthy participants has been previously demonstrated in the literature with Transcranial Magnetic Stimulation (TMS), the effects found have been inconsistent (see Pulvermüller et al., 2005; Willems et al., 2011). We note here that while some participants with motor lesions do not show such deficits on action verbs (Papeo et al., 2010; Arévalo et al., 2012; Kemmerer et al., 2012; Maieron et al., 2013), none of these studies compare verbs with and without motion components, a contrast investigated as part of this study.

It has been found that visual motion features of verb meanings recruit the posterior parietal area pSTS (for reviews see Gennari 2012 and Watson et al., 2013), but also the middle temporal area of the visual cortex (known in the literature as MT/V5 or Brodmann area 19, noteworthy for its high responsiveness to visually dynamic stimuli and relatively low retinotopy; Grill-Spector & Malach, 2004). We have previously shown MT/V5 to be involved in tasks that merely imply visual motion, such as the perception of static images depicting dynamic motion (e.g., an athlete about to kick a football; Senior et al., 2002) and other studies have revealed that it is also involved during reading tasks that contain the description of motion (e.g., "the car drives towards you"; Rüschemeyer et al., 2010), with MT activation when viewing static images also mediated by the language immediately preceding it (Coventry et al., 2013). Crucially, these studies indicate that visual motion must be strongly implied in order to activate MT/V5. No studies have yet shown this for individual words nor, as noted earlier, have necessary and sufficient conditions for its involvement in the computation of

language that describes motion been investigated. Further, previous work examining verbs typically confounds the semantic components of deliberate action and visual motion. Many of these studies use goal-directed actions when examining the recruitment of visual motion areas, and do not disentangle action from motion. Therefore, recruitment of visual motion areas may be contingent upon the verb containing an additional goal-directed action component.

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125 126 Lateral occipitotemporal cortex (which includes MT) is associated with patterns of motion, motion related artifacts such as tools and depictions of hands (Bracci et al. 2010; Bracci et al. 2012) and verbal material referring to actions symbolically (for a review see Lingnau & Downing 2015). Bedny et al. (2008) are generally cited as having shown that the activation in lateral occipitotemporal cortex associated with verbs is not due to visual motion or motor activity. That fMRI study by Bedny and colleagues contrasted high-motion verbs (concrete dynamic actions such as 'jump'), intermediate-motion verbs (change-of-state and bodily function) and low-motion verbs (states), showing that the amount of motion did not modulate activation of the lateral occipitotemporal cortex. However their low-motion verbs were states such as mental states and did not refer to agentive motionless actions such as 'holding' or 'clutching' which may indeed activate regions much more anterior to lateral occipitotemporal cortex (Kemmerer et al, 2012). Furthermore, high-motion verbs in that study by Bedny and colleagues were confounded with action, while a neater confirmation of motion associated verb activation in lateral occipitotemporal cortex would be verbs involving visual motion but not deliberate action i.e. observable events such as 'crumbling' or 'flowing'. In a later fMRI study by Peelen et al. (2012) showing that lateral occipitotemporal cortex is activated by state verbs (including mental states) and event verbs, the event verb category did not refer to observable events but again included concrete dynamic actions such as walking and running. Unlike previous studies, the current study delineates the action and motion element completely. The behavioural performance of patients who have sustained lesions in the left hemisphere is uniquely placed to inform our understanding of language processing by addressing this central issue.

Although lesion studies are not suitable to investigate discrete areas such as MT or pSTS, if we can show that defective motion processing is selectively associated with the posterior part of the brain housing MT and pSTS such as Brodmann area 19 or area 39, in contrast to the more anterior brain sparing those regions, we can infer that neuro-anatomically dissociable regions are activated when processing action or motion verbs, and that recruitment of these regions is necessary to derive meaning when processing modality-specific semantic knowledge. A second issue with respect to the possible links between language and recruitment of distinct neural correlates concerns the nature of the tasks used to test these links. 'Levels of processing' (Craik & Tulving, 1975) refers to the degree to which a participant recruits semantic knowledge: it constitutes the qualitative difference between, for example, counting the vowels in "sinking" and knowing that "sinking" and "plunging" are more similar than "flowing" and "plunging". Reviews (Taylor & Zwaan, 2009; 2012; Tomasino & Rumiati, 2013) find that the type of language task is a critical factor when determining the recruitment of specific brain regions. For example, semantic decisions ("Is GRASP an action?") affect hand movements while lexical decisions ("Is GRASP a word?") typically do not. This difference in the recruitment of alternative neural networks as a function of task requirements accounts for discrepancies within both behavioural (Lindemann et al., 2006; Sato et al., 2008) and neuroimaging paradigms (Postle et al., 2008; Kemmerer et al., 2008). In each case, a lexical, word-based decision does not result in activation of dissociable processes while a more cognitively demanding semantic task does suggesting that recruitment of neuro-anatomically dissociable regions is only necessary when generating recruiting semantic representations but not when making lexical decisions that do not rely on semantic information.

In our current design we accounted for these two critical issues by using tasks varying on semantic demand and words that entirely delineate the action and motion element. Firstly, to account for discrepancies in the data regarding recruitment of specific brain regions we included three tasks with different levels of cognitive demand. Our critical

Semantic Similarity Judgement Task (SSJT) was expected to indicate any dissociation in action/motion verb processing in patients; as the most cognitively demanding semantic task it was considered most sensitive in identifying these dissociations. An additional Verb-Picture Matching (VPM) task was administered; easier than the SSJT but also reliant on semantic processing it was included to support the SSJT in cases of more severe stroke. Both the SSJT and VPM do not present words in isolation, but instead require comparisons to be made between two verb stimuli. A final Lexical Decision task required classification of a linguistic stimulus as a word, and was expected rely on inherently more superficial processes that would not require the activation of dissociable processes.

Secondly, we delineated the action and motion element completely (see Table 1). As highlighted above verb content varies with some describing action (hitting), some not (desiring) while others describe motion (falling) and others not (holding). In the current fully factorial design, four verb types were used to assess the behavioural and neural independence of action and motion word processing. Verbs contained elements of action and motion (concrete, dynamic actions; "throwing"), action without motion (motionless actions; "holding"), motion without action (observable events; "flowing"), and neither action or motion (mental states; "hoping"). In doing so, the necessity of dissociable and neuro-anatomically separate regions during action and/or motion processing can be wholly explored.

Whilst the current study is not well placed to assess the critical role of the specific brain regions required when processing particular verbs due to diffuse lesion patterns and a sample size that does not allow voxel based lesion analysis, it can certainly confirm the importance of neural correlates. It is predicted that distinctive brain areas are recruited most reliably when a person accesses the relevant semantic dimension. If recruitment of additional brain areas is necessary when representing concepts, then damage to these areas may result in impaired processing of action and/or motion verbs. It is furthermore predicted that the predicted dissociations will be evident in the more cognitively demanding semantic tasks but not in a lexical decision task. Finally, although included to maintain a fully factorial design, we do not make predictions about the performance of patients when processing mental state verbs, as these do not include an action or motion element.

	+motion	-motion	150
	I. Concrete, dynamic	II. Motionless actions] 151
+action	actions throwing, chopping	holding, ogling	152
	III. Observable events	IV. Mental states	153
-action	crumbling, flowing	hoping, desiring	154
			155

Table 1. Example linguistic stimuli. Patients with lesions involving posterior parietal and lateral occipitotemporal cortex are predicted to be impaired on processing words representing *Observable events* but should perform normally on *Motionless action* words. In contrast, in patients with more anterior lesions sparing posterior parietal and lateral occipitotemporal cortex are predicted to be impaired on processing words representing *Motionless actions* but should perform normally on processing *Observable event* words. Impairments on *Concrete, dynamic action* can arise from either lesion location because the verb refers both to motion and action content. No prediction is made about processing verbs referring to *Mental states*.

2. Materials and Methods

2.1 Participants and lesion location

Patients. For this multiple single-case study patients were recruited from UK National Health Hospitals / Stroke rehabilitation units located in the North East of England. Hospital admissions were screened to select patients with CT evidence of a recent ischaemic infarct or haemorrhagic stroke involving the left hemisphere. Anyone with cognitive impairment (identified from hospital screening procedures e.g. Mini Mental State Examination; MMSE), known dementia, or reported substance abuse were excluded. Patients for whom significant comprehension problems were noted in the hospital notes by clinicians or speech and language therapists beyond the acute phase of stroke were not approached because they would not cope with the tasks in this study. At test, language comprehension was further evaluated through use of the Token Task and Mississippi Aphasia Screening Test (MAST) to ensure patients could complete the experimental tasks. These tests are described below in section 2.2.1. Based on this criteria twenty five participants were initially recruited as in-patients however seventeen participants could not be followed up after discharge or did not complete all of the experimental tasks of this study.

Finally, based on the radiologist's clinical CT or MRI report we identified patients with lesions implicating either the anterior or posterior portion of the left hemisphere. Using scan images we could reliably class six out of eight patients. One patient was excluded because he had lacunar infarct to the left internal capsule that did not fit either anterior or posterior pattern. A second patient (patient CC) had some early signs of left hemisphere low attenuation in an otherwise nonspecific scan not allowing for classification or later lesion analysis. She had furthermore no behavioural deficits indicating a particular lesion site. She was included in the testing nevertheless as an unclassified patient and her normal performance across the experimental tasks is documented in Table 3. Thus the individual results of six left hemisphere patients are reported in detail in this study (3 Female, age range 52-75 years, mean 68yrs 10mths, SD = 8yrs 6mths,). Patients were seen at a mean time of 45.71 days (SD 13.97) post stroke. All were able to provide informed consent.

Details of each patient's lesion as identified in the CT and/or MRI reports are described below. Table 2 also lists the Brodmann areas implicated in each patient. To determine which Brodmann areas were damaged, each patient's lesions were mapped onto the digital brain image on the basis of the radiologist's report using MRIcron software package (Rorden, Karnath, & Bonilha, 2007; http://www.mccauslandcenter.sc.edu/mricro/ mricron/). Scans were normalised (using Clinical Tool box software through SPM; Rorden, Bonilha, Fridriksson, Bender, & Karnath, 2012; http://www.mricro.com/clinical-toolbox/) and applied to the Brodmann Atlas included in MRIcron. Figure 1 includes overlaid scan slides of each patient. On the basis of scan information three patients (patients TY, MAS, and SB) were firmly classified as having more anterior lesions sparing the posterior parietal and lateral occipitotemporal regions of interest for motion verbs. Critically, two patients (patients FR and JC) had lesions involving the posterior regions of interest for motion verbs. FR had infarcts involving the left internal capsule and an old left parietooccipital lesion. JC also had lesions to the parietooccipital and lateral occipitotemporal cortex. In contrast TY had a frontal infarction that was restricted to inferior frontal and orbitofrontal territory and rostral superior and middle temporal gyrus. SB had a bleed limited to the frontal lobe. Patient MAS's lesion pattern is associated with small vessel disease affecting periventricular white matter, left temporal lobe, and left internal capsule as noted in the clinical report. As such disconnection, potentially affecting the semantic network, is probable. The multiple ill-defined white matter lesions were mostly unsuitable for mapping. However a cortical anterior lesion and small non cortical white matter posterior lesion were identified. Furthermore, based on her symptoms of motor weakness and expressive aphasia coupled with the implication of more anterior cortical areas (BA 2, 3, 4, 8, & 40) this patient for the purpose of this study was classified as an anterior patient. In relation to the research question this is justified because the lesions in this patient spared posterior parietal and lateral occipitotemporal cortex hypothesised as associated with motion comprehension... One patient (patient DH) had an extensive lesion involving both anterior and posterior parts of the left hemisphere (left frontotemporoparietal and insula) and we therefore would not expect a dissociative pattern of impairments for processing action or motion verbs in this patient. However given that DH's lesion implicated both anterior and posterior cortical areas we felt his behaviour was still relevant to the hypotheses.

 Healthy controls. A control group of fifteen healthy older adults aged 63–84 years (mean 71yrs 8mths, SD 6yrs 2mths, 9 female) were recruited from a database of older adults held in the Department of Psychology, Northumbria University. Control participants were right handed (as were patients), and had not sustained any form of stroke or other form of brain damage. The control group received £3.00 for their participation. All procedures were approved by the local Ethics Committee within the Department of Psychology, Northumbria University as well as NHS research ethics.



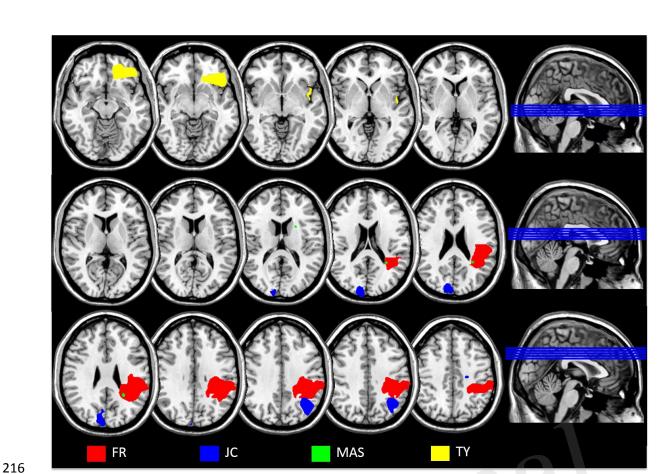


Figure 1 Overlaid scan slices of each patient applied to a template scan to allow clear visualisation of the anatomical landmarks using MRIcron software package (Rorden et al., 2007; http://www.mccauslandcenter.sc.edu/mricro/mricron/). Clinical scans could not be obtained for patient SB; the scan for DF was performed too early for the lesion to be accurately localised. Left is right as per neurological convention.

2.2 Method and procedure

Verb content varies – some involve action (hitting), some not (desiring) and some involve movement (falling), some not (holding). Because of their versatility, verbs afford firm control over semantic content and linguistic factors while tapping into different, but experimentally predictable, resources (see Table 1). The design of the current study allows an investigation of the neural systems to be involved in language comprehension. This pushes for novelty in two ways: By investigating across semantic dimensions and levels of processing.

In line with the depth-contingent processing hypothesis outlined in the introduction, we predict that non-dedicated brain areas are recruited most reliably when a person accesses the relevant semantic dimensions. Hence, anterior lesions will consistently interfere with semantic decisions on verbs describing motionless actions (A+/M-) and posterior lesions will interfere with semantic decisions on verbs describing observable events (A-/M+) only. Crucially, the more cognitively demanding semantic tasks outlined below (Semantic Similarity Judgment Task and Verb-Picture Matching; SSJT and VPM, respectively) do not present words in isolation, but in more meaningful contexts requiring comparisons to be made between stimuli; further, lexical decision merely requires classification of a linguistic stimulus

- as a word, while the semantic tasks require comparison. Each of these changes enhances the depth of semantic processing. We therefore predict effects in the more cognitively demanding tasks (SSJT and VPM), which rely more heavily on semantic processing, and not in the less cognitively demanding task, which relies on inherently more superficial processes. Further, we expect the SSJT to be more sensitive at identifying dissociations in verb processing (due to recruitment of non-dedicated brain regions) as it is more cognitively demanding than the VPM. In more severe stroke however, we expect the VPM to add insight into SSJT performance.
- 2.4.1 Screening and patient documentation
- 245 Mississippi Aphasia Screening Test (MAST)
- 246 As the participants had suffered damage to the left hemisphere, language and communication skills
- were assessed using the Mississippi Aphasia Screening Test (MAST; Nakase-Thompson, 2004). The
- 248 MAST contains nine subtests ranging from 1 10 items and provides indices of receptive and
- 249 expressive aphasia. There was a maximum score of 50 points for each of the receptive and expressive
- aphasia indices which are noted for each of the patients in Table 2.
- 251 The Token Test
- The general severity of any receptive aphasia was also assessed using the short version of the token
- test for language comprehension (De Renzi & Faglioni, 1978). As indicated in Table 2, all patients
- successfully followed commands consisting of at least five stages.
- 255 Symptoms of Apraxia and Neglect
- A standard battery of apraxia screening tests was administered to document symptoms of apraxia.
- These included imitation of hand and finger gestures (Goldenberg, 1996), whereby the patient was
- 258 required to copy a series of gestures that were demonstrated by the experimenter (pathological score
- 259 ≤ 17/20 on either task), and pantomime (Goldenberg, Hermsdörfer, Glindemann, Rorden & Karnath,
- 260 2007) and actual use (De Renzi & Lucchelli, 1988) of common objects (pathological score ≤ 43/53 and
- 261 ≤16/18 for respective tasks); the examiner named the object-use action and patients were marked on
- the presence or absence of predefined movement features. Based on the overall performance accuracy
- across all apraxic screening tests, the severity of apraxia was calculated. All patients were no less than
- 90 percent accurate across the screen except for patient MAS who was 85% accurate. Errors in patient
- MAS's performance was apparent during the imitation of hand gestures (scoring 17/20) and in the form
- of body-part-as-object errors during object-use pantomime (scoring 31/53). Pathological scores were
- also noted for FR during the imitation of finger gestures (17/20) and DH during hand gesture imitation
- 268 (15/2). Remaining patients did not obtain a pathological score during apraxia screening. Visuospatial
- 269 neglect was assessed using the Apples Test (Bickerton, Samson, & Humphreys, 2011) and is reported
- 270 in Table 2. All the above standard neuropsychological tests were examined within days of the
- 271 experimental assessment.

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Object Recognition screening task

Word stimuli were presented in preparation for the experimental session to establish that basic processing of written words and pictures were intact. For this task, participants were presented with a written one-word exemplar (uppercase, Arial font, size 72) and asked to read but not verbalise or attempt to verbalise the presented word. When the participant confirmed they had read the word, they were presented with the pictorial representation of the word amongst three distractors that belonged to the same semantic category. For example, circle (target), rectangle, triangle, and square (distractors). Participants had to identify which one of the four images they believed was a representation of the target word. This procedure was followed for four targets from different semantic categories:- an animal (rabbit), fruit (lemon), object (clock), and shape (circle). The pictorial target and distractor stimuli for each semantic category were printed in colour onto one A4 laminated sheet. The four exemplars of the aforementioned semantic categories were selected from the Snodgrass and Vanderwart (1980) set of images. None of the patients had difficulty with either of these screening tasks.

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Table 2. Documentation of each patient

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Patient at strol	Days post stroke	post weakness stroke	Aphasia noted on admission ^a	Aphasia screening (MAST) expressive/ receptive (50/50)	Language comprehension (stage reached of	Neglect/ hemianopia	Apraxia Score	Brodmann Areas damaged on basis of clinical scan (% = amount lesioned)			
	at test				Token Test)		(%) ^b	>75%	25-75%	<25%	
TY	74	49	Yes	Yes	49/50	5	No	98		47	11, 38
MAS	75	20	Yes	Yes	26/48	5	No	85			2, 3, 4, 8, 40
SB	72	50	No	Yes	50/48	5	Left allocentric neglect	99			
DH	68	56	Yes	Yes	17/48	6	No	90			
FR	81	33	Yes	No	50/49	6	No	96	2	40, 41	4, 21, 39, 42
JC	52	55	Yes	Yes	40/48	6	Right superior quadrantanopia	93		39	6, 7, 19, 40

Only the scan report details are included for DH because the scan was performed too early to allow accurate localisation of the full extent of this large lesion. The scan of SB could not be obtained for mapping but the radiologist's original report noting a frontal bleed leaves little uncertainty.

^aSymptoms noted on admission were on the basis of hospital notes written by clinicians and therapists.

^bApraxia score (%) refers to overall accuracy across apraxia screening tests: imitation (hand and finger gestures; pathological score ≤ 17/20 on either task) and object-use tasks (pantomime and actual use; pathological score ≤ 43/53 and ≤16/18 respectively) with 100% meaning no errors were made on any of the tests.

- 291 2.2.2 Experimental tasks
- 292 Word stimuli used in the Lexical task and Semantic Similarity Judgement Task (SSJT)
- 293 Common English words (between 4 – 7 letters in length) were selected and the suffix 'ing' added to
- 294 disambiguate all words as verbs. Each word was allocated to one of the four conditions (see Table 1).
- 295 Four independent assessors were provided with all verbs and the operationalised definitions of each
- 296 condition, and rated whether they agreed (Yes / No response) to each verb / condition pairing. Only the
- 297 verbs that reached a majority agreement by at least three of the four assessors were retained. A Google
- 298 search of hits for each verb was used to obtain the frequency of use in the English language. Selected
- items were matched for letter length, number of syllables, and frequency (details are given in Appendix 299
- 300 A).
- 301 In addition to the use of independent assessors, we also examined available linguistic resources to
- 302 extract information regarding imageability and concreteness for individual verbs (Wilson, 1988; Bird,
- Franklin, & Howard, 2001), and existing classifications of verbs where relevant (e.g. Levin, 1993). From 303
- 304 these resources we constructed a more limited list of verbs for final analysis: the full list and the reduced
- 305 list are in Appendix A). The reported analyses are based on the items in bold only. Of course the word
- 306 lists are supposed to differ in their ratings on some of these dimensions (e.g. a +action verb is clearly
- 307 more concrete and imageable than a -action verb).
- 308 To construct the stimuli for the SSJT – a task successfully implemented in previous research both in
- 309 neuroimaging and clinical populations (Kemmerer et al., 2008; Fernandino et al., 2013) - each word
- from the final list, referred to as the 'pivot', was matched with a word of similar meaning (target), and a 310
- 311 distractor word. Both the target and distractor were taken from the same semantic category as the pivot.
- 312 Note that distractors are consistently, but only moderately, different from pivots and targets; this requires
- participants think carefully about subtleties in the meanings of all three words in order to successfully 313
- 314 complete the task. An additional four independent raters confirmed that the target / pivot items were
- 315 more similar in meaning compared with the distractor / pivot items (see Appendix B for an exhaustive
- 316 list of pivots, targets, and distractors).
- 317 Non-word stimuli used in the Lexical task:
- 318 non-words ARC list of fifty-two was obtained from the Non-word Database
- 319 (http://www.maccs.mq.edu.au/~nwdb/nwdb.html). These followed the same letter-length criteria as the
- 320 word stimuli and were converted into verbs as described above. Thirteen non-words were allocated to
- 321 each of the four conditions, and matched with the corresponding UK English verbs for letter-length and
- number of syllables. Each non-word was novel with no repetitions across the four categories (see 322
- 323 Appendix C).
- 324 Picture stimuli used in the Verb-Picture Matching task (VPM)
- Two pictorial representations of each of the fifty-two English verbs used for the word stimuli were 325
- 326 created. A search on Google Images identified photographic representations of each verb. An

additional four independent assessors rated how closely each image represented its associated verb.

An image was allocated as the *target* pictorial representation of each verb if a majority agreement of 1st

choice was reached by at least three of the four assessors. The fifty-two images rated as 2nd choice

were retained as distractor images. Each of the fifty-two target images were randomly paired with a

distractor image from the same condition (i.e. the four conditions outlined in Table 1).

2.2.3 Procedure

All participants provided written informed consent and were tested either in hospital / rehabilitation unit, or at their own homes or university premises if they were healthy controls. Testing was completed over two or three sessions depending on how many tasks the participant could complete at each visit. All tasks were administered in a fixed order as below. The computerized tasks were presented to the participants using a Toshiba laptop with a twelve inch screen, and programmed using Eprime2. Participants were asked to identify the target by either stating this verbally or pointing to their choice. The participants' response was recorded by the experimenter using either a left or right mouse click. A 4-trial practice session was administered to ensure the participants understood the task instructions. If necessary this was repeated until the participant demonstrated they fully understood the task requirements. There was no maximum time limit and each set of stimuli was interspersed by a blank screen of no fixed duration to enable the participants to have a rest at any time they needed

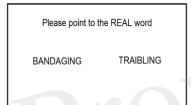






Figure 2: Screen layouts (from left to right) for the lexical decision task, semantic similarity judgment task, and the verb-picture matching task.

Lexical Decision task

The participants were presented with two words on screen; one real word and one non-word. They were asked to identify which was the real word. This task is illustrated in Figure 2. Control participants were not assessed on this basic task.

Semantic Similarity Judgement Task (SSJT)

The participants were advised that they would see one word in red coloured text (*pivot*) at the top of the screen. Underneath they would see two words (*target and distractor*) in black text. They were instructed to choose which one of the two words in black text was most similar to the word in red. Instructions stating 'Which of the two words below is most similar to the word above' were also presented on screen below the *pivot*. The pivot word was presented centrally in the upper third of the screen. The target and distractor words were presented centrally (vertically) and equidistant (horizontally) from the centre of

the screen (see Figure 2). The presentation of the target word on the left / right of the screen was counterbalanced across all trials.

Verb-picture matching task (VPM)

The stimuli consisted of one pivot word (as described in the word stimuli section) and the two pictorial representations (one target and one distractor as described in the picture stimuli section). The pivot word was presented centrally in the upper third of the screen. The target and distractor images were presented centrally (vertically) and equidistant (horizontally) from the centre of the screen. As above the participants were advised that they would see one word in black coloured text at the top of the screen. Underneath they would see two images. They were instructed to identify which one of the two images was most similar to the word above. Instructions stating 'Which picture best matches the following word' were also presented on screen above the pivot. Order of presentation of the target on the left and right of the screen was counterbalanced.

2.3. Data Analysis

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384 385 The data from six patients were included in the analyses. In order to explore the variance in individuals' performance in greater depth, a multiple single-case approach was adopted. The patients' task performance on the experimental tasks was compared to that of the healthy control group using modified t-tests (Crawford & Garthwaite, 2002), a standard statistical analysis which enables significance testing of individual scores compared with a control group. This method has been shown to be robust when comparing single-cases to a small control sample even in instances where such a sample is not normally distributed (Crawford, Garthwaite, Azzalini, Howell, & Laws, 2006). All patients completed the lexical, SSJT, and VPM tasks and where possible patients were retested on the critical SSJT task to confirm the pattern of results; whilst the VPM was useful for adding clarity to noisy data in cases of severe stroke, the more cognitively demanding SSJT was believed to most reliant on the activation of semantic processes when making action/motion decisions. Retest took place 3 months after initial testing on the task (on average across patients retest took place 14 weeks and 3 days after initial testing). It was not possible to retest two of the six patients (patient MAS and SB) as they were not reachable after discharge. The scores on SSJT in Table 3 are those at first testing, and any changes at retest are accounted for in text where available for individual patients.

3. Results

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Overall, the patients demonstrated dissociable deficits for action or motion verbs depending on lesion location. Inspection of the combined averaged percentage correct from initial and retest of the SSJT task (see individual results for details of duration between test / retest) for each condition identified patients with more anterior lesions sparing posterior parietal and lateral occipitotemporal cortex (TY, MAS, SB) making more errors in the motionless action (+Action/-Motion) condition (t=-3.631, p=.001) whilst the patients with lesions involving posterior parietal or lateral occipitotemporal cortex (FR & JC) made significantly more errors in the observable event (-Action/+Motion) condition (t=-3.631, p=.001).

To explore a dissociation of semantic representations for action and motion specific verbs, differences in performance on the semantic tasks (SSJT & VPM) were compared between individual patient scores and the normative data from the healthy control participants (see Table 3). The performance of patients classed as having anterior lesions are initially discussed followed by those classed as having posterior lesions.

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Patient	SSJT			Verb-Picture Matching			Lexical					
(lesion)	+A+M	+A-M	-A+M	-A-M	+A+M	+A-M	-A+M	-A-M	+A+M	+A-M	-A+M	-A-M
CCa	92	100	92	100	100	100	100	100	100	92	100	100
TYb	100*,1	67**	100	67**	100	100	100	80	100	100	100	100
MASb	89	67**	100	100	100	100	100	80	89	100	100	100
SBb	78*	83*	100	100	78**	83**	100	60**	89	100	100	83
DHd	33**	67**	17**	83*	100	83**	83**	80	100	100	100	83
FR°	89	100	83*	67**	100	100	100	80	100	100	100	100
JC ^c	78*	100	50**	83*	100	75**	100	50**	89	100	100	100
Controls (SD)	88(5)	99(4)	97(7)	97(7)	100(0)	100(0)	100(0)	88(12)	n.t.	n.t.	n.t.	n.t.

Table 3. Patient percentage correct for the semantic tasks on the SSJT at initial testing, the VPM, and the Lexical Decision task. Dark shaded areas in the table highlight the expected pattern of impairments, and light shaded areas highlight the expected dissociating intact performance. *p<.05; **p<.001; 1patient performance better than control group. a unclassified lesion (patient scan too early to identify lesion); b more anterior lesions sparing posterior parietal and lateral occipitotemporal cortex; c lesions involving posterior parietal and/or lateral occipitotemporal cortex; d widespread left hemisphere lesion including both posterior and more anterior regions of interest.

Analysis of the results from initial testing of the Semantic Similarity Judgement Task (SSJT) confirmed that patients with more anterior lesions sparing posterior parietal and lateral occipitotemporal cortex (TY, MAS, SB) showed significantly impaired performance in the motionless action (+Action/-Motion) condition compared to control participants, suggesting a deficit in action comprehension, while performing normally on the observable event (-Action/+Motion) condition. Individual patient performance is as follows:

Patient TY (expect impaired processing of action verbs).

Lesion and deficits. TY had a frontal infarct implicating BA 47, 11 and 38; presented with aphasia and motor weakness on admission; at test he had no symptoms of expressive or receptive aphasia and no symptoms of visual neglect or apraxia.

SSJT. A robust deficit was observed for processing motionless action (+Action/-Motion) items of the SSJT task at initial and retest (11 weeks, 4 days later) when compared to the control group (both t=-7.746, p<.001). TY was significantly impaired in the mental states (-Action/-Motion) category compared to control participants in both SSJT testing sessions (both t=-4.150, p=<.001). TY performed at ceiling on the observable event (-Action/+Motion) condition at initial testing (t=0.415, p=.342). TY was also unimpaired in the +Action/+Motion condition, performing better than controls on both test and retest sessions in this condition (both t=2.324, p=.018). Of note, at retest TY's performance was impaired in

- 426 the -Action/+Motion condition (t=-7.746, p<.001). This is difficult to interpret, but is not considered 427 indicative of a motion processing impairment given his perfect performance in this condition in the VPM
- and at initial SSJT test. 428
- 429 VPM. TY's performance was at ceiling for the two critical conditions (+Action/-Motion and -
- 430 Action/+Motion) as well as on +Action/+Motion (t=0.00, p=ns) and comparable to controls on the mental
- 431 state (-Action/-Motion) condition (t=-0.645, p=ns).
- Interpretation. Performance at ceiling during the VPM does not allow interpretation, but based on SSJT 432
- 433 performance it can be concluded that TY's performance on the initial and retest of the SSJT suggest a
- 434 robust deficit specific to motionless actions (+Action/-Motion), in keeping with what was predicted on
- 435 the basis of this patients frontal lobe infarction, sparing posterior parietal and lateral occipitotemporal
- cortex associated with motion comprehension. 436

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- Patient MAS (expect impaired processing of action verbs).
- 439 Lesion and deficits. Lesion implicated periventricular white matter, left temporal lobe, left internal
- 440 capsule (BA 2, 3, 4, 8, 40); presented with aphasia and motor weakness on admission; at test she had
- 441 no symptoms of neglect but demonstrated expressive aphasia and mild apraxic symptoms.
- 442 SSJT. Compared to controls, MAS showed a distinct impairment in the motionless action (+Action/-
- 443 Motion) condition: t=-7.746, p<.001; performance on remaining verb conditions were comparable to
- controls (see Table 3). Patient MAS' performance was at ceiling on the observable event (-444
- 445 Action/+Motion) condition: t=0.415, p=.342, and mental state (-Action/-Motion) condition: t=0.415
- 446 p=.342, and comparable to controls in the concrete, dynamic action (+Action/+Motion) condition:
- 447 t=0.194, p=.425.
- 448 VPM. MAS' performance was at ceiling for the two critical conditions (+Action/-Motion and -
- 449 Action/+Motion) as well as on the concrete, dynamic action (+Action/+Motion, t=0.00, p=ns) and
- 450 comparable to controls on the mental state condition (-Action/-Motion t=-0.645, p=ns).
- 451 Interpretation. In conclusion, based on highly selective impairment in the critical motionless action
- 452 condition of the SSJT task this patient's performance, like the above patient, is in keeping with what
- 453 was predicted on the basis of this patients more anterior lesion. Based on her post-stroke behavioural
- impairments and her lesion data, it is possible that disconnection, potentially affecting the semantic 454
- 455 network, has occurred in this patient. Posterior parietal and lateral occipitotemporal cortex associated
- 456 with motion comprehension are however spared.

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Patient SB (expect impaired processing of action verbs).

459 Lesion and deficits. SB had a frontal bleed; aphasia was observed on admission, with no symptoms of 460 motor weakness; at test, SB showed no symptoms of aphasia or apraxia but demonstrated left allocentric neglect. 461

SSJT. SB performed poorly in the critical motionless action (+Action/-Motion) condition (t=-3.873, p=.001). Performance in the concrete, dynamic action (+Action/+Motion) condition was also lower than controls (t=-1.936, p=.037). Performance was comparable to controls in the observable event (-Action/+Motion) condition (t=0.415, p=.342). There was no difference between SB and the control groups performance in the mental state (-Action/-Motion) condition (t=0.415, p=.342)

VPM. Consistent with the SSJT, SB performed worse than controls in the motionless action (+Action/-Motion) condition (t=-16.460, p<.001) and the concrete, dynamic action (+Action/+Motion) condition (t=-21.301-14.254, p<.001). Unlike the SSJT, SB was significantly impaired in the mental state (-Action/-Motion) condition (t=-2.259, p=.002). Performance was comparable to controls in the observable event (-Action/+Motion) condition (t=0.00, p=ns).

Interpretation. Although SB was impaired on a number of verb conditions, the dissociation between impaired motionless action (+Action/-Motion) comprehension and intact comprehension of observable events (-Action/+Motion) was clearly evident based on the combined SSJT and VPM performance in this patient. This was predicted based on the frontal bleed sparing posterior parietal and lateral occipitotemporal cortex,

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Patient DH (expect impairment in processing either / both action / motion verbs).

Lesion and deficits. DH suffered a significant stroke leaving him quite impaired; aphasia and right motor weakness were noted on admission and at test DH had severe expressive aphasia, but no visual neglect or apraxia. His clinical scan was performed very early on; too early to reliably localise the lesion. Based on the radiologist's report describing a lesion in the left fronto-temporo-parietal infarct and insula and his disfluent speech indicative of a frontal lesion, DH was classed as both anterior and posterior. It was therefore predicted that this patient would not present a neat dissociation in verb processing performance. This wide-spread damage also seems to be reflected in his non-specific behaviour on the experimental tasks.

SSJT. DH performed poorly across this task on initial test and retest, which may be attributable to the severity of his stroke. At both initial and retest, DH was significantly less accurate across all conditions compared to the control group (all p≤.037). Initial testing did not reveal a clear pattern of behaviour (see Table 3); DH showed the most notable deficit in the observable event (-Action/+Motion) condition (t=-11.066, p<.001) followed by the concrete, dynamic action (+Action/+Motion) condition (t=-10.651, p<.001). At retest and still significantly impaired compared to the controls, DH's performance improved in both the observable event (-Action/+Motion) and concrete, dynamic action (+Action/+Motion), but fared considerably worse in the motionless action (+Action/-Motion) condition.

495 VPM. Unlike the SSJT, DH's behaviour on the less demanding VPM task showed more specific deficits. 496 Compared to controls, DH's performance was significantly poorer in the motionless action (+Action/-497 Motion) condition (t=-16.460, p<.001) as well as on and the observable event (-Action/+Motion) 498 condition (t=-16.460, p=<.001). In contrast performance was normal on concrete dynamic action 499 (+Action/+Motion; t=0.00, p ns) and in the mental state (-Action/-Motion; t=-.645, p=.265) condition. 500 Interpretation. Although the pattern of results with this patient is somewhat clouded by a general level 501 of impairment (i.e. performing poorly across many conditions on the more demanding SSJT task) it is 502 interesting that this patient on the VMP was impaired only on the two critical experimental conditions 503 observable events associated with posterior damage and motionless actions associated with more 504 anterior damage, while managing normal performance on the other two conditions of the VPM task 505 concrete dynamic action and mental states. In conclusion, this patient showed the non-selective pattern 506 of behaviour predicted by his lesion involving both areas of interest. 507 508 Patient FR (expect impairment in processing motion verbs). Lesion and deficits. Lesion implicated the left internal capsule and left parieto-occipital region (BA 40, 509 510 41 4, 21, 39, 42); aphasia on admission without right motor weakness; at test FR had no symptoms of 511 aphasia, neglect, or apraxia. 512 SSJT. FR showed poor performance in the critical observable event (-Action/+Motion) condition at initial test (t=-1.936, p=,037) and retest (t=-4.150, p<.001) 21 weeks 6 days later, suggesting a robust motion 513 514 deficit (see Table 3). Performance on the mental state (-Action/-Motion) condition at initial testing (t=-515 4.150, p<.001) and retest (t=-1.936, p=.037) was significantly poorer than controls. Normal performance 516 was however observed in the motionless action (+Action/-Motion; t=0.242, p=.406) and the concrete, 517 dynamic action (+Action/+Motion; t=0.194, p=.425) conditions compared with controls. *VPM.* FR's performance was comparable to controls across conditions (all $p \ge .265$), performing largely 518 519 at ceiling. This may be indicative of his mild stroke. 520 Interpretation. A distinct -Action/+Motion deficit with maintained +Action/-Motion and +Action/+Motion 521 performance in the SSJT suggests that FR presented with an isolated deficit in the comprehension of 522 motion verbs in line with a lesion involving posterior parietal cortex.

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526 527 Patient JC (expect impairment in processing motion verbs).

Lesion and deficits. Parieto-occipital infarct implicating BA 39, 6, 7, 19, 40; aphasia, right motor weakness and right superior quadrantanopia on admission; at test showed mild expressive aphasia but no symptoms of apraxia.

- 529 6.501, p<.001) and retest (t=-4.150, p<.001) 11 weeks 4 days later. Impaired performance was also
- observed at initial and retest in the concrete dynamic action (+Action/+Motion): both t=-1.936, *p*=.037,
- and mental state (-Action/-Motion) condition: both t=-1.936, p=.037. JC's performance was equivalent
- to the control participants at both the initial test and retest in the motionless action (+Action/-Motion)
- 533 condition (both t=0.242, *p*=.406).
- 534 VPM. Unlike SSJT, JC performed significantly worse in both the motionless action (+Action/-Motion; t=-
- 535 24.206, p<.001) and mental state (-Action/-Motion; t=-3.066, p=.004) conditions compared with the
- 536 control group. Performance was comparable to controls for the dynamic action (+Action/+Motion) and
- observable event (-Action/+Motion) conditions (both t=0.00, *p*=ns).
- 538 Interpretation. Although the contrast between this patient's performance on the SSJT and VPM tasks
- 539 introduces an element of uncertainty, it is worth noting that performance on the VPM task was not
- reflected in other tasks. On the basis of the SSJT task performance at both initial test and retest this
- 541 patient presented with a dissociation between impaired comprehension of motion associated
- observable events and intact comprehension of motionless actions, in line with this patient's lesion
- 543 involving both posterior parietal cortex and lateral occipitotemporal cortex.
- 544 Lexical decision task
- As predicted, the pattern of dissociations was evident on the semantic task, but not the lexical
- 546 processing task. Patients performed worse than the healthy control participants in the semantic tasks
- and these deficits were selective across the action present / motion present conditions. Conversely,
- 548 patients performed accurately in the lexical decision tasks and showed hit rates substantially higher
- compared to hit rates in the semantic tasks, with patients performing at ceiling or making very few
- 550 errors.
- To summarise the pattern of dissociations, patients with more anterior lesions sparing posterior parietal
- 552 cortex and lateral occipitotemporal cortex (TY, MAS, & SB) were consistently poorer on tasks involving
- verbs describing motionless actions (+Action/-Motion). On the other hand, patients with lesions
- involving posterior parietal cortex and lateral occipitotemporal cortex (FR, JC) were consistently poorer
- on tasks involving verbs describing observable events (-Action/+Motion), while patient DH with a large
- lesion involving both areas of interest did not show dissociate behaviour.
- 557 4. Discussion
- In conditions where verbs contained action and/or motion content, patients with lesions involving
- 559 posterior parietal and lateral occiptotemporal cortex show a selective deficit on semantic decisions
- regarding verbs that afford motion. Patients with lesions sparing these posterior regions associated with
- motion processing showed the opposite pattern of selective deficits in action verb processing but intact
- motion verb processing. The dissociation between action and motion routes to verb understanding is
- 563 important. In past studies verbs depicting actions have been considered primarily in relation to

motor/premotor activations – but actions depict motions as well as actions. For that reason, the variable results found in past studies may partly be a function of two routes to understanding verbs – action and motion. In the patients we have found dissociations between verbs affording motion-only and verbs affording action-only in cognitively demanding semantic tasks. The opposite pattern of results was seen in patients where posterior regions associated with motion were spared: these patients performed poorly on verbs affording actions but not motion while they performed well on verbs affording action but not motion. Whilst in this small sample we cannot perform detailed lesion analyses, the fact that this selectivity is associated with specific anterior/posterior lesion patterns has implications for most assumptions about action verb understanding, indicating multiple routes to comprehension. This would be consistent with recent work on understanding goals and intentions through actions, with evidence that motor/premotor system activation might be one of several routes to action understanding (Eshuis, Coventry, & Vulchanova, 2009; Gredebäck & Melinder, 2010).

Most broadly, these results contribute to our understanding of language processing as an integrated phenomenon that involves the contribution of knowledge representation from a wide variety of sensorimotor modalities (Barsalou, 1999; Taylor et al., 2008), converging with the perspective (Binder & Desai, 2011; Yee, Chrysikou, & Thompson-Schill, 2013) that semantic knowledge is distributed across brain areas corresponding to the sensory-functional and sensorimotor characteristics of the referent. In this respect, our findings converge with findings from a variety of methodological approaches demonstrating overlapping neural substrates between language and the motor cortex, including transcranial magnetic stimulation (TMS; Pulvermüller et al., 2005; Buccino et al., 2005), magnetoencephalography (MEG; see Hauk et al., 2008 for review), fMRI (Kemmerer et al., 2012), and behavioural studies (see Glenberg et al., 2013 for a review). Our results most closely relate to those of TMS paradigms, as the temporary "artificial lesions" created in healthy participants in a TMS study are reflected in the natural lesions of our sample of participants, allowing us to draw inferences about the substantive contribution these brain areas make to semantic decisions.

All patients in the current study performed at ceiling level on the lexical decision task, which required identification of a real word against a pronounceable and equivalent non-word distractor (e.g., "praying" vs "pibbling"). This suggests that a lexical decision does not rely on the recruitment of alternative neural networks. The predicted pattern of dissociations was evident however in the more cognitively demanding semantic tasks. The word-based SSJT task, in which required participants to decide whether "praying" was more similar to "wishing" or "judging", was distinctly affected by the different brain lesions that were revealed by the patients studied here. To a large extent results from the picture-based VPM, which required participants to identify a picture for example of a person praying, mirrored those observed in the SSJT for verbs containing an action and/or motion content. Whilst easier than the word-based SSJT but also reliant on semantic processing, the VPM added clarity to poor performance on the SSJT. In particular, patient DH who had suffered a severe stroke, was consistently poor across conditions of the SSJT but only showed poor performance on the critical conditions of the VPM with normal performance on the neutral conditions. Together, performance across the three tasks emphasises that recruitment of dissociable neural processes is dependent upon task requirement and

cognitive demand, which may explain discrepancies found in previous data (Lindemann et al., 2006; Kemmerer et al., 2008; Postle et al., 2008; Sato et al., 2008).

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It is worth noting that while the patients show statistically reliable, specific, and robust deficits in the predicted semantic categories, these selective impairments were remarkably subtle and not a reflection of typical aphasia, with receptive performance on the diagnostic screening for aphasia (MAST) near ceiling level (scoring 48 out of 50 or above) for most of our patients. Similarly, all patients performed near ceiling on the lexical decision task, with aggregate accuracy over 95%. These results promote awareness that language deficits resulting from stroke may be subtler than previously imagined, or assumed by current diagnostic material.

At the same time it should be noted that language is usually studied in cognitive psychology laboratories removed from language in the real world. Seeing the word 'STOP' on a red sign at a busy traffic intersection is quite different from seeing the word STOP in black text on a white background in an experimental psychology laboratory and as such laboratory based work may lack the ecological validity required to fully understand the cognitive mechanisms that mediate natural language (e.g., Zwaan, 2009). Thus differing aspects of context, motivation, and task may result in drastically different psychological and neurophysiological responses. The choice of language task has serious implications for the identification of language problems. Cognitively demanding semantic tasks are more useful for identifying more distributed neural networks associated with language processing as lexical decisions may not require the recruitment of dissociable brain regions. Further, one of the hallmarks of language is its contextual versatility – from identification of words to conversations requiring extensive inferences and social comprehension. The latter, more semantically rich, contexts are particularly important to tap in neuropsychological testing, as exactly these tasks recruit more distributed neural networks. The current finding that specific parts of the distributed network give rise to selective impairments resonates with an emerging proposal in the cognitive sciences holding that the brain areas and networks associated with an event are a function of context, task, and strategies, not simply constrained within the domain of a particular stimulus (Tomasino & Rumiati, 2013; Bracci et al. 2015). Indeed it emerges that recruitment of several neural networks may be critical to derive meaning from language.

As predicted semantic representations for concrete, dynamic action verbs may be associated with lesions either related to action or motion processing. Indeed, we did not find the selective association with lesion location that we found for motionless events in posterior patients and observable events not associated with bodily action in patients with more anterior lesions. Perhaps more interesting, we did see impairments on processing verbs representing mental states in a number of patients who were not impaired on some of the other verb categories but as predicted without an associated lesion pattern. Although this leaves open the possibility that semantic content regarding motionless and 'actionless' mental states is behaviourally and neurally independent from other verbs, this falls outside the remit of the investigation focussed on the independence of action and motion representation and its relationship to posterior parietal and lateral occipitotemporal cortex. Nevertheless, representations for verbs describing mental events in particular are left unresolved, as in previous work by Peelen et al. (2012)

for example, mental state verbs like 'she believes' were mixed in with state verbs such as 'she is liked', 'he lies down' or 'she equates'. To what extent do verbs referring to mental states rely on visual and motor systems? Existing theories and results on this are particularly conflicted (Postle et al., 2007; Ruschemeyer et al., 2008; Gallese & Lakoff, 2005; Vigliocco et al., 2009; Dove, 2010). With regard to current results, it is worth highlighting that the data comes from patients with such mixed lesion patterns do not generate results that are entirely clear cut, as is often the case with neuropsychological research.

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A further inherent weakness of the current study – and potentially an area for improvement in future – concerns the selection criteria for items. First, the observable events category contains a small number of lexical items, placing an artificial constraint on the number of verbs possible in the present study. Second, natural confounds exist between verb classes with; for example, observable events should inherent have higher imageability and concreteness ratings than mental events. This may also account for poor performance in verbs representing mental states in some patients. During the SSJT, four of the six patients performed significantly worse than controls when processing mental state verbs, which was consistent for two of these patients (SB & JC) in the Verb-Picture Matching task. Control participants also showed a drop in performance in the mental state condition of the VPM compared to other conditions. It is likely that the abstractness of these –Action/-Motion verbs, particularly in pictorial form, is generally more difficult to process, resulting in reduced performance in the mental state condition. Nevertheless, we reiterate that performance during mental state decisions cannot be used to evaluate dissociations when processing verbs involving action or motion and therefore do not discredit our other findings in the remaining stimuli. Third, only four raters assessed our categorization - and even they failed to reach a universal consensus on the full list of items. In the present study, then, we faced an inherent trade-off between statistical power and experimental validity. In future, perhaps more robust selection criteria - for example, including imageability and concreteness ratings for fewer stimuli that enjoy more universal agreement on category - might shift the balance towards improved methodological rigour at the expense of statistical power.

Establishing whether similar effects can be found in healthy participants with artificially-induced "lesions" is critical to demonstrating that these brain regions are in fact essential to action understanding in healthy populations (Taylor & Zwaan, 2009). However the current study is limited by a small sample size preventing the identification of specific non-dedicated cortical regions being determined. Further study would require a larger sample to enable voxel based lesion analyses to pinpoint the critical role of specific brain regions when processing action/motion verbs. The current results must therefore be considered within the larger context of behavioural and neuroscience research (e.g. Lingnau & Downing 2015). Most immediately the current experimental design and hypotheses lend themselves to replication, both in other patients and in healthy participants who take part in transcranial magnetic stimulation (TMS) protocols in the way we delineated motion and action dimensions completely. Such results would bolster the claims here, showing that they are neither patient centred artefacts nor a bias of stroke victims more broadly. Note, however, that over time patients may well develop alternative routes to understanding – a point that TMS cannot speak to.

679 Recent advances in imaging analyses using connectivity analysis will afford investigation of the interplay 680 between action and motion processing regions. Such interplay may allow us to explain when +Action/+Motion verbs are preserved or impaired in patients with specific lesions and furthermore reveal 681 682 potential differential representation of the interesting Mental States verb category. 683 Neuroimaging work with healthy participants has identified brain activity mapping onto discrete cortical 684 areas for action, motion, contact, and state change (Kemmerer et al., 2008). Previous neuropsychology 685 research has demonstrated a dissociation between action verbs, which tend to be impaired by anterior 686 lesions, and concrete nouns which are impaired by posterior lesions (Neiniger & Pulvermüller, 2003). 687 One of the key contributions of the present work is to elucidate the causality behind these effects and 688 to demonstrate a dissociation within a lexical category. Future work may consider the causality of such 689 activity and build an account of "abstract" concepts, even if this begins with an account of verbs that 690 are not both concrete and have an immediate sensory or bodily referent. 691 References 692 Andrews, M., Vigliocco, G. & Vinson, D. P. (2009). Integrating experiential and distributional data to 693 learn semantic representations. Psychological Review, 116(3), 463-498. 694 Arévalo, A.L., Baldo, J,V. & Dronkers, N.F. (2012). What do brain lesions tell us about theories of 695 embodied semantics and the human mirror neuron system? Cortex, 48(2), 242-254... 696 Bak, T. H., Yancopoulo, D., Nestor, P.J., Xuereb, J.H., Spillantini, M.G., Pulvermüller, F. & Hodges, J. 697 R. (2006). Clinical, imaging and pathological correlates of a hereditary deficit in verb and 698 action processing. Brain, 129(2), 321-332. 699 Barsalou, L.W. (1999). Perceptual symbol systems. Behavioral and Brain Sciences, 22, 577-609. 700 Bedny, M., Caramazza, A., Grossman, E., Pascual-Leone, A., Saze, R. (2008). Concepts are more 701 than percepts: The case of action verbs. Journal of Neuroscience, 28(44), 11347-11353. 702 Bickerton, W-L., Samson, D., & Humphreys, G. W. (2011). Separating forms of neglect using the 703 Apples Test: Validation and functional prediction in chronic and acute stroke. 704 Neuropsychology, 25(5), 567-580. 705 Binder, J. R. & Desai, R. H. (2011). The neurobiology of semantic memory. Trends in Cognitive 706 Sciences, 15(11), 527-536.

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Appendices

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Appendix A: Full set of word stimuli presented for each of the four Action and Motion categories of each task. Only items in bold were retained for analysis after we removed a number of items that were not deemed to be clear-cut based on available linguistic resources to extract information regarding imageability and concreteness for individual verbs (Wilson, 1988; Bird, Franklin, & Howard, 2001), and existing classifications of verbs where relevant (Levin, 1993).

	Concrete, dynamic actions	Motionless actions	Observable events	Mental states
	bandaging	attending	blooming	advising
	banging	bargaining	clattering	amending
	chopping	clasping	crumbling	appointing
	Cutting	clinging	drifting	banishing
	digging	clutching	floating	desiring
	mopping	drooping	flowing	doubting
	rubbing	embracing	lurching	emitting
	scratching	holding	plunging	hoping
	scribbling	lighting	printing	liking
	squashing	loitering	slipping	blessing
	throwing	ogling	slumping	pondering
	tossing	slouching	wilting	praying
	waxing	storing	yawning	wishing
Length	7.84	8.23	8	7.84
Syllables	2.15	2.38	2.15	2.54
Frequency	70,302,000	87,420,300	86,483,385	74,729,000
Bold items				
Length	8.11	7.83	8	7.33
Syllables	2.22	2.17	2.17	2.33
Frequency	86,176,222	134,243,333	64,316,667	102,316,667

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Concrete, dynamic action (+A+M)

Motionless action (+A-M)

Pivot word	Target	Distractor	Pivot word	Target	Distractor
bandaging	wrapping	peeling	attending	watching	Glancing
banging	whacking	pricking	bargaining	haggling	Buying
chopping	dicing	scraping	clasping	clinging	storing
cutting	slicing	mashing	clinging	clutching	Saving
digging	shovelling	carving	clutching	squeezing	Touching
mopping	scrubbing	chopping	drooping	slouching	Leaning
rubbing	massaging	tearing	embracing	hugging	Greeting
scratching	rubbing	tapping	holding	gripping	Touching
scribbling	scrawling	writing	lighting	igniting	Switching
squashing	smashing	flicking	loitering	waiting	Lounging
throwing	tossing	catching	ogling	staring	Peeking
tossing	flinging	scraping	slouching	drooping	Tilting
waxing	polishing	scrubbing	storing	saving	Switching
Obse	ervable event (-/	A+M)	M	ental state (-A-N	M)

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Observable event (-A+M)

	9 / 1 ''			•	•
Pivot word	Target	Distractor	Pivot word	Target	Distractor
blooming	blossoming	sprouting	advising	suggesting	Insulting
clattering	rattling	rumbling	amending	changing	Doubting
crumbling	breaking	creasing	appointing	hiring	Arguing
drifting	floating	lurching	banishing	condemning	Hating
floating	drifting	clattering	blessing	praising	Recalling
flowing	coursing	resting	desiring	wanting	Liking
lurching	slumping	blooming	doubting	opposing	Altering
plunging	sinking	flowing	emitting	shining	Drifting
printing	copying	falling	hoping	wishing	Enjoying
slipping	tripping	limping	liking	approving	Blessing
slumping	lurching	falling	pondering	thinking	remembering

	wilting	withering	crumbling	praying	wishing	Enjoying
	yawning	snoozing	reading	wishing	hoping	Thinking
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874 Appendix C: Word / Non-word pairing for the lexical task

Concrete, dynamic actions (+A+M)		Motionless actions (+A+M)			ole events +M)	Mental states (-A-M)		
Target	Distractor	Target	Distractor	Target	Distractor	Target	Distractor	
bandaging	traibling	attending	skoreling	blooming	twusting	advising	tarbling	
banging	macting	bargaining	glickering	clattering	spromining	amending	bawthling	
chopping	snaiting	clasping	twafting	crumbling	knarbling	appointing	aflurnting	
cutting	geebing	clinging	stedging	drifting	fanching	banishing	vourating	
digging	pooting	clutching	spaicking	floating	whesping	desiring	seegling	
mopping	lunting	drooping	smatting	flowing	draling	doubting	cronzing	
rubbing	zeeging	embracing	quartling	lurching	smarsing	emitting	deetling	
scratching	spreliching	holding	linzing	plunging	keedging	hoping	Futing	
scribbling	brouttling	lighting	scolting	printing	foolting	liking	rebing	
squashing	thrudding	loitering	sleebling	slipping	phurbing	blessing	skebbing	
throwing	jurnging	ogling	ebling	slumping	floosing	pondering	knarbling	
tossing	veffing	slouching	dringling	wilting	nosting	praying	linzing	
waxing	lejing	storing	merning	yawning	sloning	wishing	touning	