The role of conflict, feedback, and action comprehension in monitoring of action errors: Evidence for internal and external routes

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Abstract

The mechanisms and brain regions underlying error monitoring in complex action are poorly understood, yet errors and impaired error correction in these tasks are hallmarks of apraxia, a common disorder associated with left hemisphere stroke. Accounts of monitoring of language posit an *internal route* by which production planning or competition between candidate representations provide predictive signals that monitoring is required to prevent error, and an *external route* in which output is monitored using the comprehension system. Abnormal reliance on the external route has been associated with damage to brain regions critical for sensory-motor transformation and a pattern of gradual error 'clean-up' called *conduite d'approche (CD)*. Action pantomime data from 67 participants with left hemisphere stroke were consistent with versions of *internal route* theories positing that competition signals monitoring requirements. Support Vector Regression Lesion Symptom Mapping (SVR-LSM) showed that lesions in the inferior parietal, posterior temporal, and arcuate fasciculus/superior longitudinal fasciculus predicted *action conduite d'approche*, overlapping the regions previously observed in the language domain. A second experiment with 12 patients who produced substantial action CD assessed whether factors impacting the internal route (action production ability, competition) versus external route (vision of produced actions, action comprehension) influenced correction attempts. In these 'high CD' patients, vision of produced actions and integrity of gesture comprehension interacted to determine successful error correction, supporting *external route* theories. Viewed together, these and other data suggest that skilled actions are monitored both by an internal route in which conflict aids in detection and correction of errors during production planning, and an external route that detects mismatches between produced actions and stored knowledge of action appearance. The parallels between language and action monitoring mechanisms and neuroanatomical networks pave the way for further exploration of common and distinct processes across these domains.

1. <u>Introduction</u>

The ability to monitor one's own behavior to detect and repair errors early in their production is critical to fluid, adaptive behavior. The mechanisms underlying monitoring and correction of errors in complex limb actions (such as movement imitation, tool use, or tool pantomimes) have received little scientific attention and are poorly understood. In that context, research on error monitoring in the motor control and speech domains provide useful frameworks within which we can begin to understand complex action monitoring.

Classical accounts of motor control assumed that sensory feedback was used to correct errors after they occurred. It has long been appreciated, however, that correction of errors may occur too rapidly to be attributable to visual feedback. For example, suppression of erroneous movements in visually guided tracking has been observed as early as 20-40 milliseconds after movement onset (Cooke & Diggles, 1984). Additionally, nascent incorrect hand responses ("partial errors") may occur in choice reaction time tasks before correct responses are produced, likely reflecting the on-line detection, inhibition and correction of erroneous responses (Meckler, Carbonnell, Ramdani, Hasbroucq, & Vidal, 2017). To explain such data, it has been proposed that a copy of the motor planning signal is used to generate a prediction of expected sensory feedback. When actual feedback poorly matches the prediction, an error signal is generated and monitored to allow rapid modification of the motor plan (e.g., Desmurget & Grafton, 2000; Kawato, 1999; Wolpert & Miall, 1996).

In the language domain, considerable evidence suggests that errors may be monitored in several ways. First, there is evidence that the comprehension system plays a role in detection of produced errors (*external monitoring*). For example, language production suffers when neurotypical speakers are asked to detect their own errors while their productions are noise-masked (Lackner & Tuller, 1979; Oomen, Postma, & Kolk, 2001; Postma & Noordanus, 1996). However, at least some monitoring and repair occurs too rapidly to be the result of comprehension of one's own utterances (Levelt, 1983). This suggests that planned speech may be monitored prior to actual production, either through the monitoring of "inner speech" and/or via the operation of the production system (both are forms of *internal monitoring*) (Postma, 2000). Inner speech monitoring may operate on abstract phonological representations activated during relatively early stages of speech planning. In contrast, monitoring of the production system is thought to occur during a later stage entailing planning of articulation. In this case, the

anticipated sensory consequences of planned articulatory movements may be calculated via a forward model, and any mismatches between predicted and actual outcomes used as a signal that correction is needed (Tian & Poeppel, 2015). Importantly, while most forward model theories posit monitoring of the comparison between predicted feedback (generated via efference copy of motor commands) and actual sensory feedback, Pickering and Garrod (2013) propose that monitoring of internal representations and comparison with target representations occurs at several stages prior to and during actual motor planning. We will return to the question of the planning stage at which internal monitoring may occur at several points below.

Finally, a specific subset of internal monitoring accounts proposes that monitoring is based on the detection of a requirement to select between competing alternatives, such that monitoring is increased when selection is difficult (*conflict monitoring*; Nozari, Dell, & Schwartz, 2011). In speech production, conflict monitoring is thought to occur both at motor planning stages supporting articulatory selection, as well as at earlier processing levels. In support of the latter possibility, recent data suggest that the magnitude of an electrophysiological signature of conflict monitoring, the error-related negativity, is influenced by the closeness of the semantic relationship between linguistic target and competitor stimuli (e.g., Ganushchak & Schiller, 2008), suggesting that selection difficulty during lexical-semantic processing (i.e., not just in motor planning) may signal a monitoring requirement.

Computationally-influenced models of error monitoring and correction have been especially useful in elucidating the possible mechanisms of conduction aphasia, characterized by phonological speech errors in the context of relatively intact auditory comprehension. A particular hallmark of conduction aphasia is *conduite d'approche* (CD), successive responses that often entail some degree of phonological improvement, but which may or may not end with a correct response (Baldo, Klostermann, & Dronkers, 2008; Damasio & Damasio, 1980; Goodglass, 1992). For example, when asked to repeat the word "violin", one conduction aphasic produced the responses "vel, vela, velet, vel, vely, velinet" (Franklin, Buerk, & Howard, 2002). CD has long been thought to reflect monitoring and error detection using the comprehension system (i.e., *external monitoring*), with repeated attempts at phonological correction necessitated by an impaired articulatory planning system. When comprehension is intact, speakers are able to detect mismatches between their own productions and an internal representation of what the target should sound like; once a match is achieved, the CD episode can terminate (Goodglass,

1992). Broadly consistent with this possibility, lesions to the arcuate fasciculus (often considered to be a portion of the superior longitudinal fasciculus; hereafter AF/SLF) is classically associated with conduction aphasia, and consistent with a disconnection of intact temporally-mediated comprehension from other stages/aspects of language production planning.

A more recent model focuses not on disconnection, but on an impairment of the processes by which auditory "targets" (a representation of what speech output should sound like) are used to inform motor plans to achieve those sounds. On this account, conduction aphasia is related to damage to a region within the sylvian fissure at the parietal-temporal boundary (area SPT) known to be critical to auditory–motor integration (Hickok & Poeppel, 2004). Following from this, Walker and Hickok (2015) tested a computational approach in which conduction aphasia was modeled as a weakened internal predictive system associated with impaired auditory to motor transformation. The model simulations suggested that the characteristic conduite d'approche behavior is a compensatory behavior in which auditory feedback is relied upon when the predictive system fails.

In contrast to the motor control and language domains, few studies have addressed the mechanisms of complex action monitoring or its neuroanatomical substrates. In that context, research on skilled typing is instructive. The dominant account suggests that monitoring of typing errors depends upon the cooperation of a relatively slow outer loop and a nested, rapid inner loop. The outer loop encodes the intended word and monitors visual feedback (i.e., the displayed word) to detect mismatches with the intended word, whereas the inner loop automatically and rapidly detects mismatches between planned single key presses (generated via communication with the outer loop) and haptic feedback from the keys (e.g., Snyder, Logan, & Yamaguchi, 2015). Thus, the typing literature is in broad agreement with the language literature in specifying both external and internal routes to monitoring.

Typing is a highly overlearned motor task requiring a limited set of sequences of finger movements, and it is unclear whether and how monitoring in that domain is relevant to the monitoring of complex limb actions such as tool use pantomime and imitation. Pantomime and imitation are particularly important because they are the hallmarks of limb apraxia, a common but poorly understood left hemisphere syndrome. Furthermore, unlike the speech and motor domains, there is not (to our knowledge) a clear account of how limb action error monitoring occurs or the mechanisms causing its disruption in states of divided attention or in neurological

disorders (Humphreys, Forde, Francis, Carlson, Sohn, & Burgess, 2000; Giovannetti, Schwartz, & Buxbaum, 2007). In that context, there are two relevant observations. First, errors in pantomime and imitation in limb apraxia are further aggravated by the removal of vision of the patients' hands (Jax, Buxbaum, & Moll, 2006), suggesting that error monitoring and correction in apraxia may rely abnormally upon external visual feedback[1]. Second, patients with limb apraxia may produce CD (Watson & Buxbaum, 2015; Luzzi, Piccirilli, Pesallaccia, Fabi, & Provinciali, 2010; Smania, Girardi, Domenicali, Lora, & Aglioti, 2000).

Particularly strongly motivating our interests in this study, we previously observed that CD in apraxia on a pantomime to sight of objects task was significantly more frequent with objects associated with two conflicting actions than with objects associated with a single canonical action (Watson & Buxbaum, 2015), potentially consistent with *conflict monitoring* accounts. Moreover, apraxics' continued effort to correct their errors suggested at least some residual monitoring ability. Finally, although high rates of errors in apraxia were associated in part with AF/SLF lesions, neither behavioral nor neuroanatomic analyses in the prior study were specifically focused on CD. We here performed two experiments to align the previous disparate observations about the factors influencing error monitoring and correction in complex limb actions with the substantially more developed accounts of error monitoring and correction in the language and motor domains, and to better understand the neuroanatomic basis for abnormalities in complex action monitoring.

In the first experiment with 67 left hemisphere stroke patients, we assessed the hypothesis that we would observe sensitivity to action conflict in the genesis of CD, which we defined here as *error trials with correction attempts*. We also explored the neuroanatomic substrates of this behavior, predicting that lesions to the AF/SLF and/or temporo-parietal junction (TPJ, which includes area SPT) may be predictive of error correction attempts. Though SPT is thought to be specialized for audio-motor integration, and therefore would not be expected to play a role in limb error monitoring, proximal TPJ/peri-sylvian regions including inferior angular and supramarginal gyri and posterior superior temporal lobe are thought to support sensorimotor

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[1] Patients with apraxia are more accurate with real object use than in pantomime tasks, suggesting that the somatosensory and kinesthetic feedback associated with object use may also be beneficial in reducing errors (Randerath, Goldenberg, Spijkers, Li, & Hermsdorfer, 2011). We focus here on visual feedback; the impact of other forms of feedback on monitoring behavior will be of interest for future study.

integration (e.g., Huang & Sereno, 2018; Matsumoto, Misaki, & Miyauchi, 2004) and may be expected to be critical to limb error monitoring. A secondary hypothesis, derived from *conflict monitoring* accounts, was that lesions to the IFG, important for error detection (Gauvin, De Baene, Brass, & Hartsuiker, 2016) would *decrease* the likelihood of error correction attempts[2].

In the second experiment, we specifically selected 12 patients who produced numerous error correction attempts, with the aim of delving more deeply into the factors influencing CD. Specifically, we assessed the importance of external visual feedback, action comprehension, and action production skills in influencing the likelihood that an error – once produced—would be followed by a correction attempt. To anticipate one of our results, we also sought to replicate the role of conflict seen in Study 1 using a different paradigm. As error correction attempts may sometimes occur without ultimately successful error repair (Franklin et al., 2002), we also assessed the influence of visual feedback, action comprehension, and action production on a second dependent measure -- *Successful Corrections* -- defined as a correction attempt episode ending in a correct response.

We generated several predictions. Production-based *internal monitoring* accounts predict a relationship between the integrity of the production system and the propensity for error correction attempts, but no relationship with action comprehension. *External monitoring* accounts predict that patients will produce more correction attempts (and perhaps, more successful corrections) when visual feedback is available *and* the action comprehension system is intact. In contrast, there should be no effect of the integrity of the production system. Finally, *conflict monitoring* accounts predict that the likelihood of error correction attempts should increase in conditions placing greater demands on selection.

2. **General Methods**

2.1 Participants

Sixty-seven chronic left hemisphere stroke survivors (more than 6 months post-stroke) were recruited from the Neuro-Cognitive Rehabilitation Research Registry at Moss Rehabilitation Research Institute (Schwartz, Brecher, Whyte, & Klein, 2005) (45% female, mean

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[2] Conflict monitoring accounts make the additional prediction that lesions to the anterior cingulate will produce monitoring deficits; as cingulate cortex is in the territory of the anterior cerebral artery, we are unable to test this prediction in our subjects, the great majority of whom had suffered middle cerebral artery stroke.

age = 59 years, SD = 11, mean education = 14 years SD = 3). Demographic information and scores on the experimental tasks in Experiment 1 are shown in Table 1. Patients with a history of psychosis, neurologic disorder, traumatic brain injury, or drug abuse were excluded. To ensure that patients understood task instructions, patients with severely impaired verbal comprehension (score < 4 on comprehension subtest of the Western Aphasia Battery; Kertesz, 1982) were also excluded. Patients were not specifically selected for presence or severity of apraxia. Action comprehension data and pantomime data from 31 patients were previously reported (Watson & Buxbaum, 2015). In compliance with the guidelines of the Institutional Review Board of Einstein Healthcare Network, all patients gave informed consent and were compensated for travel expenses and participation. The informed consents obtained did not include permission to make data publicly available.

Table 1. Patient demographic and behavioral task information for Experiment 1.

Subject ID	Gender	Handed-ness	Age	Education	Months Post-stroke	Lesion Volume (ml^3)	Pantomime Accuracy (% correct)	Number of Error Correction Attempts	Percent Error Trials with Error Correction Attempts
1	M	R	54	11	172	50394	96	5	45
2	M	R	64	11	140	181620	89	5	38
3	M	R	58	13	149	99980	83	4	17
4	F	R	55	16	185	115118	88	10	45
5	M	R	79	13	143	95662	85	1	6
6	F	R	47	12	156	48305	96	1	17
7	M	R	68	19	174	258736	82	1	5
8	M	R	63	12	114	69778	85	6	25
9	M	R	79	12	129	144857	74	0	0
10	F	R	52	16	120	78357	96	0	0
11	M	R	67	13	94	16091	94	0	0
12	M	R	38	12	90	16964	98	2	33
13	M	R	54	13	80	166393	93	12	67
14	M	R	74	13	88	99569	95	0	0
15	F	R	75	12	84	20190	88	6	26
16	M	R	68	19	60	76301	87	1	6

Subject ID	Gender	Handed-ness	Age	Education	Months Post-stroke	Lesion Volume (ml^3)	Pantomime Accuracy (% correct)	Number of Error Correction Attempts	Percent Error Trials with Error Correction Attempts
17	M	R	56	19	80	171128	78	9	31
18	M	R	80	21	105	51780	95	6	46
19	M	R	74	20	51	38651	96	3	38
20	M	R	54	14	53	82964	87	1	6
21	F	R	62	14	49	33183	84	2	8
22	F	R	54	14	68	37091	97	4	57
23	F	R	77	12	75	16547	82	4	19
24	M	R	57	12	83	17706	99	0	0
25	M	R	51	14	40	5350	79	8	31
26	F	R	51	13	126	80020	93	6	43
27	M	L	66	16	45	225021	67	16	55
28	F	R	59	16	41	200508	91	7	37
29	M	R	59	12	98	47442	99	9	69
30	M	R	60	15	54	179606	79	11	44
31	M	R	57	12	32	23141	87	18	69
32	M	R	57	21	66	20105	99	0	0
33	F	R	61	16	27	71022	86	14	58
34	M	R	68	14	28	64793	77	9	30
35	F	R	33	19	31	62204	85	8	32
36	F	R	63	12	60	14349	97	4	67
37	F	R	49	12	105	94536	96	2	29
38	F	R	68	12	50	297340	70	13	39
39	F	R	76	12	65	61198	89	7	33
40	F	R	49	12	77	131776	85	15	61
41	F	R	69	12	17	8737	88	1	6
42	M	R	49	14	36	52416	83	5	22
43	F	R	53	19	19	6840	89	6	33
44	M	R	58	12	102	85091	92	0	0
45	F	R	57	12	51	128897	93	2	18
46	F	R	34	12	55	139402	78	7	26
47	M	R	65	20	46	51399	92	0	0
48	M	R	69	19	23	71905	78	22	63
49	F	R	52	12	24	20052	94	0	0
50	F	R	68	12	49	51430	74	12	44

Subject ID	Gender	Handed-ness	Age	Education	Months Post-stroke	Lesion Volume (ml^3)	Pantomime Accuracy (% correct)	Number of Error Correction Attempts	Percent Error Trials with Error Correction Attempts
51	M	R	35	13	53	88046	95	9	64
52	M	R	58	16	42	136565	85	6	35
53	M	R	51	12	41	92744	93	2	17
54	M	R	62	12	42	200079	89	9	50
55	F	R	70	19	23	171724	81	2	8
56	F	R	42	19	11	26714	97	0	0
57	F	R	42	16	17	68764	89	1	7
58	M	R	63	14	13	60457	65	1	3
59	M	R	53	13	12	190665	99	0	0
60	F	R	42	12	23	117809	78	17	68
61	M	R	67	21	9	72630	90	10	50
62	M	R	50	11	16	16977	93	2	25
63	F	R	65	13	25	32684	89	7	41
64	F	R	68	12	15	30414	93	2	15
65	F	R	60	15	87	202614	83	3	13
66	M	R	45	18	8	64375	98	0	0
67	F	R	37	14	12	93628	96	6	36

2.2 Gesture Pantomime Task

2.2.1 Stimuli

Forty photographs of manipulable objects with a distinct use action (tools) were included in gesture pantomime tasks in Experiments 1 and 2. These objects included carpentry tools (e.g. hammer), household articles (e.g. teapot), school supplies (e.g. scissors), and grooming items (e.g. razor) drawn from the BOSS database (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010). Stimuli are available at https://sites.google.com/site/bosstimuli/. In a previous study (Watson & Buxbaum, 2015), normative data on these items were collected from 14 neurologically intact adults who were asked to rate on a 1-10 scale "the extent to which the hand movements that you make to use the object differ from the hand movements that you make to pick it up". Participants also rated these items on a scale of 1-5 by "the degree to which the shape of the object implies how it should be used" in order to measure affordance strength. Familiarity

and name agreement ratings from the BOSS database (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) were also retrieved. Using the hand movement ratings, the objects were divided into two groups: 20 "high conflict" (grasped and used with differing hand postures) and 20 "low conflict" tools (grasped and used with a similar hand posture, see Figure 1). These tools differed significantly on average conflict rating, $t(38) = 10.00$, $p < .0001$, but did not differ in terms of affordance strength, $t(38)=1.50$, $p = .14$, name agreement, $t(38) = 1.13$, $p = .26$, or familiarity, $t(38) = 1.5$, $p = .13$. For additional details on stimulus selection, grouping, and norming, see Watson and Buxbaum (2015).

Fig. 1. Examples of low conflict (A) and high conflict (B) tools used in the Experiments.

2.2.2 Gesture coding

Gesture production was recorded by digital camera and scored offline by one of two trained coders who were reliable with one another (Cohen's Kappa = 94%). These coders also obtained at least 85% agreement with previous coders in our lab (Buxbaum, Kyle, & Menon, 2005). Each trial was scored for whether or not a semantic error was present (gesture appropriate for a related object), and if not, subsequently scored on 4 spatiotemporal dimensions (hand posture, arm posture, amplitude, and timing) according to detailed praxis scoring guidelines long

in use in our laboratory (see Buxbaum, Giovannetti, & Libon, 2000 for details). If errors were observed for any of the 4 spatiotemporal components, the gesture was considered incorrect.

Separate coding guidelines were used to score error correction attempts. On trial in which the initial response was an error, we assessed whether there was also a "multiple response" – that is, multiple hand postures during a single pantomime[3]. Multiple responses were not scored when additional hand postures were produced after a participant was reminded of task instructions or if the differing postures were recognizable portions of a canonical action sequence (e.g. toothpaste application prior to the target gesture toothbrushing). We assessed the proportion of trials with an initial error that were followed by additional responses in Experiment 1, as described below.

3. <u>Experiment 1</u>

3.1 Methods

<u>3.1.1 Pantomime Task Procedure</u>

In each trial of the pantomime task, patients sat approximately 24 inches from a computer monitor and viewed a 600 x 600 pixel color photograph of a tool on the screen subtending a visual angle of approximately 40˚. The patients were asked to "show how you would use the object". Given the frequent occurrence of right hemiparesis in left hemisphere stroke, patients pantomimed using their left hands. Four practice trials with experimenter feedback regarding accuracy were given, following (Gonzalez Rothi et al., 1991). Under these guidelines, if a patient pantomimed as if his/her hand were the tool itself (e.g. pantomiming scissors as if the fingers were the blades) the patient was reminded to pantomime as if actually holding the object in their hand. Patients were only cued the first time an error of this type was made. Tool order was randomized.

<u>3.1.2 Behavioral Data Analysis Approach</u>

Behavioral data in both Experiments were analyzed using the statistical programming environment R (R Core Team, 2014). Trial level binary data were submitted to a series of mixed-effect logistic regressions using GLMER (Bates, Maechler, Bolker, & Walker, 2015). Mixed effect logistic regression is advantageous in this data set as, unlike other linear models, it does

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[3] Previous research in our laboratory has indicated that the hand posture component is the most sensitive to deficit (see Watson & Buxbaum, 2015) and most likely to be associated with discrete, distinguishable multiple responses.

not assume equal trial-level variance between participants, accepts trial-level data, and permits differing numbers of trials across subjects. It also reduces the chance of overfitting as it maximizes penalized quasi-log-likelihood (Jaeger, 2008). Intercepts for subjects and items (stimuli) were entered as random effects in Experiment 1. p-values were obtained by mapping the log likelihood ratio of the full and the reduced models with degrees of freedom equal to the number of parameters in each model onto a chi square distribution with one degree of freedom. 0.05 was used as the threshold for statistical significance. Parameter estimates are also reported with their standard errors.

The R analysis code can be viewed at https://sites.google.com/view/howardcode/home.

The dependent measure in Experiment 1 was *error correction attempts:* the proportion of error trials that were multiple response trials (i.e., in which an error was followed by additional responses). Following numerous other investigators (e.g., Kohn & Smith, 1990; Goodglass, 1992; Hickok, Houde, & Rong, 2011), we take *error correction attempts* to be an index of monitoring. Participants produced an average of 5.4 error correction attempt trials (range 0 – 22).

To explore effects of competition, tool conflict (high vs. low) was entered as a fixed effect in the mixed effect logistic regression model. To control for effects of stroke severity, and following prior studies (e.g., Fujiwara, Schwartz, Gao, Black, & Levine, 2008), the square root of each patient's lesion volume was also entered as a fixed effect. Semantic errors and deviance from given instructions (e.g. the use of both hands) caused 2.6% of trials to be excluded from the analysis.

3.1.3 Neuroimaging Acquisition and Analysis Methods

Research-quality structural MRI (n=55) or CT (n=12) scans were acquired for all patients. Research MRI scans included whole-brain T1-weighted MR images collected on a 3T (Siemens Trio, Erlangen, Germany; repetition time = 1620 msec, echo time = 3.87 msec, field of view = 192 × 256 mm, 1 × 1 × 1 mm voxels) or 1.5T (Siemens Sonata, repetition time = 3,000 msec, echo time = 3.54 msec, field of view = 24 cm, 1.25 × 1.25 × 1.25 mm voxels) scanner, using a Siemens eight-channel head coil. Patients for whom MRI scanning was contraindicated underwent whole-brain research CT scans without contrast (60 axial slices, 3–5 mm slice thickness) on a 64-slice Siemens SOMATOM Sensation scanner.

For high-resolution MRI scans, lesions were manually segmented on the patients' T1-weighted structural images. Lesioned voxels, consisting of both grey and white matter, were

assigned a value of 1 and preserved voxels were assigned a value of 0. Binarized lesion masks were then registered to a standard template (Montreal Neurological Institute "Colin27") using a symmetric diffeomorphic registration algorithm (Avants, Epstein, Grossman, & Gee, 2008, www.picsl.upenn.edu/ANTS). Volumes were first registered to an intermediate template comprised of healthy brain images acquired on the same scanner. Then, volumes were mapped onto the "Colin27" template to complete the transformation into standardized space. To ensure that no errors occurred during the transformation process, lesion maps were subsequently inspected by a neurologist (H.B. Coslett), who was naïve to the behavioral data. Research CT scans were drawn directly onto the "Colin27" template by the same neurologist using MRIcron (http://www.mccauslandcenter.sc.edu/mricro/mricron/index.html). For increased accuracy, the pitch of the template was rotated to approximate the slice plane of each patient's scan. This method has been demonstrated to achieve high intra- and inter-rater reliability (Schnur et al., 2009).

Support Vector Regression-Lesion Symptom Mapping (SVR-LSM) was performed with a MATLAB toolbox (https://cfn.upenn.edu/-zewang/) with error correction attempts as the dependent measure. SVR-LSM (Zhang, Kimberg, Coslett, Schwartz, & Wang, 2014) is a multivariate technique that uses machine learning to determine the association between lesioned voxels and behavior when considering the lesion status of all voxels submitted to the analysis. It overcomes several limitations of voxel-based lesion symptom mapping (VLSM), including inflated false positives from correlated neighboring voxels (Pustina, Avants, Faseyitan, Medaglia, & Coslett, 2018), Type 2 error due to correction for multiple comparisons (Bennett, Wolford, & Miller, 2009), and uneven statistical power due to biased lesion frequency as a function of vascular anatomy (Mah, Husain, Rees, & Nachev, 2014; Sperber & Karnath, 2017). SVR-LSM has been shown to be superior to VLSM when multiple brain areas are involved in a single behavior (Herbet, Lafargue, & Duffau, 2015; Mah et al., 2014). As with VLSM, SVR-LSM cannot accommodate binary trial-level data, thus, proportion of error correction attempts was calculated for each patient.

Voxels lesioned in less that 10% of patients were excluded. To avoid the concern that patients with larger lesions might drive results, lesion volume was regressed on both behavioral and neuroanatomical data. This method has been shown to be the most sensitive form of lesion volume correction (see DeMarco & Turkeltaub, 2018). Significance values were obtained using

1,000 permutations of the dependent measures, and a voxel-wise significance threshold of p < .05 was applied. A cluster-size threshold of 200mm^3 was also applied (Grajny et al., 2016). The number of significant voxels in each Automated Anatomical Labeling (AAL) region was calculated and is reported as a percentage of the total voxels in each region. The Johns Hopkins University Tractographic Atlas (ICBM DTI-81 Atlas; Mori et al., 2008) and ICBM template were used to identify significant voxels in the superior longitudinal fasciculus (SLF) as defined by the probabilistic map thresholded at 25% probability. The percentage of significant voxels and the coordinates of peak beta values in the AAL and ICBM regions were calculated using the SPM toolbox in MATLAB.

None of the study procedures or analyses were pre-registered prior to the research being conducted.

3.2 Results

3.2.1 Behavioral Results

The mixed-level statistical model revealed that error correction attempts were significantly more likely with high conflict items than with low conflict items, $\chi2$ (1)= 10.00, p=.002, Estimate= .45, SE= .14. There was no effect of lesion volume, $\chi2$ (1)= .44, p= .51, Estimate= .1, SE= .15.

3.2.2 Neuroanatomical Results

An SVR-LSM analysis revealed several significant clusters that, when lesioned, were associated with high proportions of error correction attempt trials. The angular gyrus (AG), supramarginal gyrus (SMG), posterior superior temporal gyrus (STG), posterior middle temporal gyrus (MTG), inferior parietal lobe (IPL), parietal operculum, middle occipital gyrus (MOG), and superior longitudinal fasciculus (SLF) were strongly associated with error correction attempts (See Table 2 and Figure 2).

A second SVR-LSM revealed that several significant clusters were associated with *low* proportions of error correction attempt trials. The caudate, putamen, inferior frontal gyrus (IFG) pars triangularis, anterior MTG, and anterior STG were associated with reduced error correction attempts (see Table 3 and Figure 2).

Table 2. Results of SVR-LSM analysis. Peak voxels and percent damage to regions with clusters > 200mm^3 voxels associated with high proportion error correction attempt trials identified by Automated Anatomical Labeling (AAL) and Johns Hopkins University Tractographic Atlas. *Note that the AAL system identifies IPL as the portion of the parietal lobe inferior to the intraparietal sulcus, superior to the angular and supramarginal gyri, and posterior to primary sensory cortex.

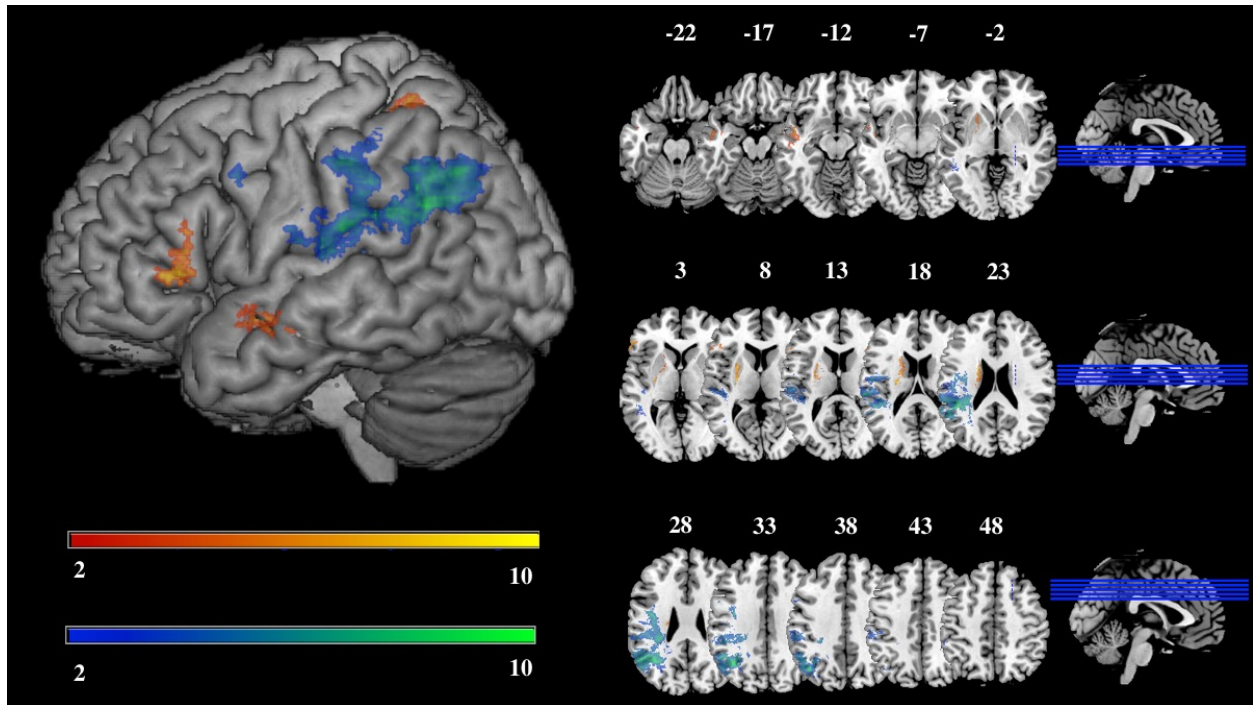| Region	Peak Voxel in Region	Number of Voxels mm^3	% of Region	Peak β
angular gyrus	(-51, -56, 26)	4,421	47.47%	9.57
superior temporal gyrus	(-44, -39, 23)	3,491	19.07%	9.66
supramarginal gyrus	(-45, -42, 23)	2,717	27.43%	10.00
middle occipital	(-36, -66, 36)	1,116	4.29%	8.78
Inferior parietal lobule (excluding SMG and AG)*	(-33, -60, 38)	1,078	5.54%	7.29
Rolandic operculum	(-41, -35, 23)	1,050	13.23%	7.36
postcentral gyrus	(-48, -17, 23)	786	2.53%	6.67
middle temporal gyrus	(-53, -46, 22)	648	1.65%	8.43
precentral gyrus	(-46, -4, 21)	415	1.47%	7.74
insula	(-34, -9, 21)	295	1.96%	7.17
superior longitudinal fasciculus	(-40, -8, 27)	2,654	40.17	9.35

Fig 2. SVR-LSM analysis of voxels significantly associated with high (blue-green) and low (red-yellow) proportions error correction attempt trials, cluster-thresholded at 200mm^3. Color bar denotes significant β values > 3.05 (blue-green) or 3.00 (red-yellow) (p < .05, permutation corrected).

Table 3. Results of SVR-LSM analysis with low proportion error correction attempt trials. Peak voxels and percent damage to regions with clusters > 200mm^3 significant voxels identified by Automated Anatomical Labeling (AAL) and Johns Hopkins University Tractographic Atlas.

Region	Peak Voxel in Region	Number of Voxels mm^3	% of Region	Peak β
putamen	(-27, 4, 7)	801	10.09%	6.59
middle temporal gyrus	(-51, -6, -18)	474	1.20%	5.44
inferior frontal gyrus, pars triangularis	(-58, 27, 4)	465	2.31%	6.59
caudate nucleus	(-19, 11, 21)	432	5.62%	7.36
superior temporal gyrus	(-49, 1, -11)	313	1.71%	6.10

3.3 Discussion

Data from Experiment 1 demonstrated that error correction attempts were significantly more likely with stimuli associated with conflicting responses. Moreover, IPL, posterior MTG, and SLF regions, when lesioned, were associated with error correction attempts. These data suggest, first, that response competition may play a role in action error detection, and second, that the brain regions associated with conduite d'approche in the language domain are also associated with this behavior in the action domain. Finally, IFG, putamen, and anterior MTG lesions tended to be associated with *fewer* error correction attempts. We will expand on these points in the General Discussion.

Because many participants included in Experiment 1 produced no CD, in Experiment 2 we selected a subgroup of patients who demonstrated moderate to severe CD in order to delve more deeply into the factors that influenced whether errors are monitored and successfully corrected. In particular, we aimed to examine the effects of external visual feedback, action comprehension, and action production ability on monitoring (error correction attempts) and successful error correction.

Prior evidence from our own work (e.g., Jax et al., 2006) and others (Haaland, Harrington, & Knight, 1999; Laimgruber, Goldenberg, & Hermsdorfer, 2005) suggests that absence of visual feedback disrupts the ability of patients with apraxia to produce correct action responses. An outstanding question is whether lack of visual feedback influences error monitoring and correction attempts, as examined in the context of CD. In addition, the relationship between visual feedback benefit and action comprehension is unknown. *External monitoring* accounts suggest that a feedback-dependent route to monitoring and correction should only be successful to the degree that action comprehension is intact; that is, when there is an existing "target" representation of the action against which the patient's own produced response can be matched (e.g. Walker & Hickok, 2015). In contrast, production-based *internal monitoring* accounts predict a relationship with action production skills, no particular deficit in the absence of visual feedback, and no particular relationship between visual feedback and action comprehension.

4. <u>Experiment 2</u>

4.1 Methods

4.1.1 Participants

To look more closely at influences on CD behavior, we selected patients who had produced CD at levels above the group mean (i.e., > 5.4 correction attempt trials) in Experiment 1. There were 12 such individuals (42% female, mean age = 58 years, SD = 14, mean education = 14 years SD = 2). Demographic information as well as scores on the experimental tasks can be found in Table 4.

Table 4. Demographic and behavioral task information for patients in Experiment 2.

Subject ID	Gender	Age	Handedness	Education	Months Post-Stroke	Experimental Task Accuracy (% correct)	Action Comprehension (% correct)	Action Production (% correct)
1	F	56	R	16	192	92	92	75
2	M	59	R	13	133	96	100	85
3	M	60	R	12	104	93	75	75
4	M	62	R	12	79	98	88	68
5	F	77	R	12	76	85	74	63
6	M	35	R	13	54	94	64	68
7	F	43	R	12	41	88	67	73
8	F	37	R	16	16	93	96	90
9	M	72	R	19	45	86	90	63
10	F	53	R	13	143	95	88	80
11	M	65	R	12	123	93	86	70
12	M	73	R	14	85	86	84	65

4.1.2 Action Comprehension Task

To examine the role of the action comprehension system in monitoring and successful error correction, we administered our laboratory's well-studied action comprehension task (see Kalenine, Buxbaum, & Coslett, 2010). On each of 24 trials, participants viewed a verb phrase describing a common action (e.g., "combing hair") on a computer screen while the experimenter read the phrase aloud. After a 2-sec delay, two videos of an experimenter performing

pantomimed actions played in succession. The participant was told to select the video (labeled "A" or "B") that matched the action phrase. The incorrect choice was an action performed with a spatial or temporal error. To ensure that patients understood the verb phrases of the action comprehension test, a verb comprehension pretest was administered requiring matching of tools with action names (e.g., matching the verb "hammering" to a depicted hammer given a choice of 3 tools). The pretest had 24 trials. Actions that patients failed on the pretest were excluded from computation of the action comprehension score.

4.1.3 Action Production Task

To index spatiotemporal gesture production skills on a task not requiring access to action knowledge, patients imitated 10 meaningless videotaped movements designed to be temporal and spatial analogs of meaningful gestures. Patients were shown each gesture twice and permitted to produce the gesture at any time during the trial. Responses were recorded with a digital camera and later scored on 4 spatiotemporal components: hand posture, arm posture, amplitude and timing by reliable coders (see Buxbaum et al., 2000, for details of the task and scoring).

4.1.4 Main Experimental Task

4.1.4.1 Procedure

Patients viewed color photographs of the same 40 tools (20 high conflict, 20 low conflict) shown in Experiment 1 and pantomimed the use of the tools using their left hands. Each image was displayed for either 3000 or 5000 ms on a computer monitor, after which a tone sounded and a blank screen replaced the image[4]. The patients were asked to pantomime the use of the tool at the sound of the tone; performance was untimed. Patients wore PLATO liquid crystal goggles (Translucent Technologies Plato System, Toronto, Canada). On half the trials, the goggles occluded with the sound of the tone, preventing vision of the limb. Exposure duration was counterbalanced across two sessions. Before the experiment began, patients pantomimed four practice items. If patients pantomimed as if their hand was the tool itself they were reminded to pantomime as if they were holding it. Patients were only given this reminder on the first occurrence. Each of the 4 practice items and 40 experimental items was shown twice per session,

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[4] Two exposure durations were included to assess the possibility that planning time would affect CD. However, no significant or trend-level effects of exposure duration were observed with any dependent measure, so we collapse across the two levels of this factor in all of the analyses reported.

once with and once without visual feedback. Item order and visual feedback order were also counterbalanced across session.
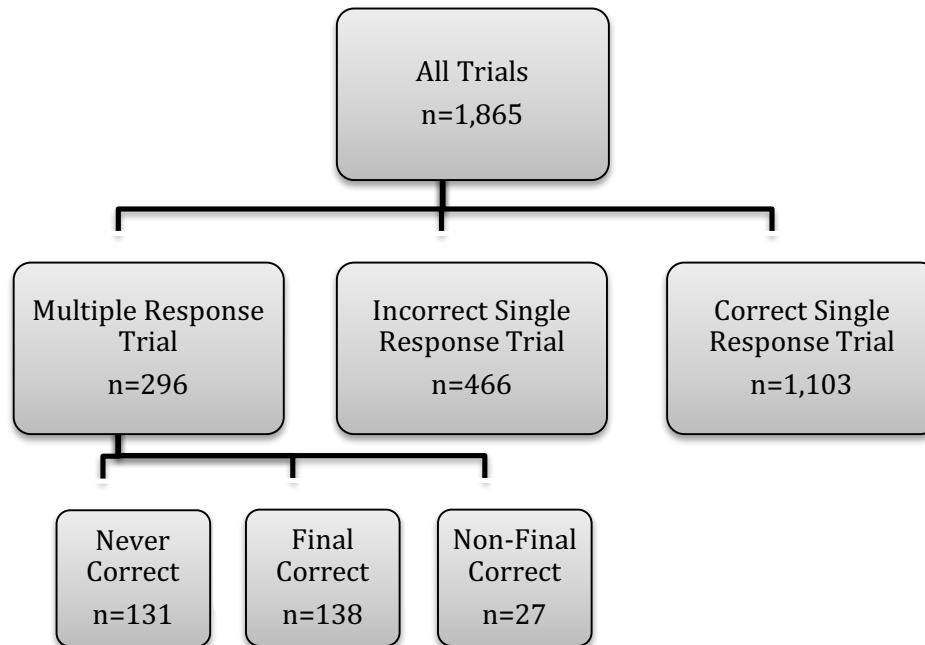
4.1.4.2 Behavioral data Coding

Pantomimes were coded for overall *spatiotemporal accuracy* (based on hand posture, arm posture, amplitude and timing) and *correction attempts* as in Experiment 1. To examine whether error correction attempts were successful, these trials were then categorized as never correct (all responses on trial incorrect), final correct (last response correct), or non-final correct (correct followed by incorrect response). Inter-rater reliability was high (Cohen's Kappa = 91%).

4.1.5 Data Analysis Approach

A total of 160 trials were coded per participant. Semantic errors and deviance from given instructions (e.g. the use of both hands) necessitated exclusion of 3% of trials. We examined two binary dependent measures focusing on monitoring and successful error correction. The first, as in Experiment 1, was *error correction attempts*, an index of monitoring. Error correction attempts were defined as error-on-first-attempt, followed by additional responses, compared to errors without additional responses (together, 41% of all trials). In addition, we assessed *successful error correction*: multiple response trials with error-on-first attempt that *ended* in a correct response (*final correct*) versus those that solely contained errors (*never correct*) (together, 16% of all trials). Non-final correct trials, in which a correct response was "sandwiched" between error responses, were infrequent (9% of all multiple response trials), and were dropped from further consideration due to their unreliability for statistical analyses. Supplementary Figure 1 shows a breakdown of all possible trial types, and their observed frequencies.

Visual feedback, conflict, action comprehension, and gesture production were entered as fixed effects in two mixed-effect logistic regressions.

Supplementary Fig. 1. Breakdown of categorization of possible trial types in Experiment 2.

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                          ┌─────────────────┐
                          │   All Trials    │
                          │   n=1,865       │
                          └────────┬────────┘
           ┌───────────────────────┼───────────────────────┐
  ┌────────┴────────┐    ┌──────────┴──────────┐   ┌────────┴────────┐
  │Multiple Response│    │   Incorrect Single  │   │  Correct Single │
  │      Trial      │    │    Response Trial   │   │  Response Trial │
  │     n=296       │    │       n=466         │   │     n=1,103     │
  └────────┬────────┘    └─────────────────────┘   └─────────────────┘
    ┌──────┼──────┐
┌───┴──┐ ┌──┴───┐ ┌──┴─────┐
│Never │ │Final │ │Non-Final│
│Correct│ │Correct│ │Correct │
│n=131 │ │n=138 │ │ n=27   │
└──────┘ └──────┘ └────────┘
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4.2 Results

4.2.1 Error Correction Attempts

In the first statistical model, we tested the factors influencing *error correction attempts*. As shown in Table 5 and Figure 3, visual feedback significantly increased the likelihood of *error correction attempts*. However, there were no effects of conflict, action comprehension, or action production.

Table 5. Influence of visual feedback, conflict, action comprehension, and action production on error correction attempts and successful error correction.

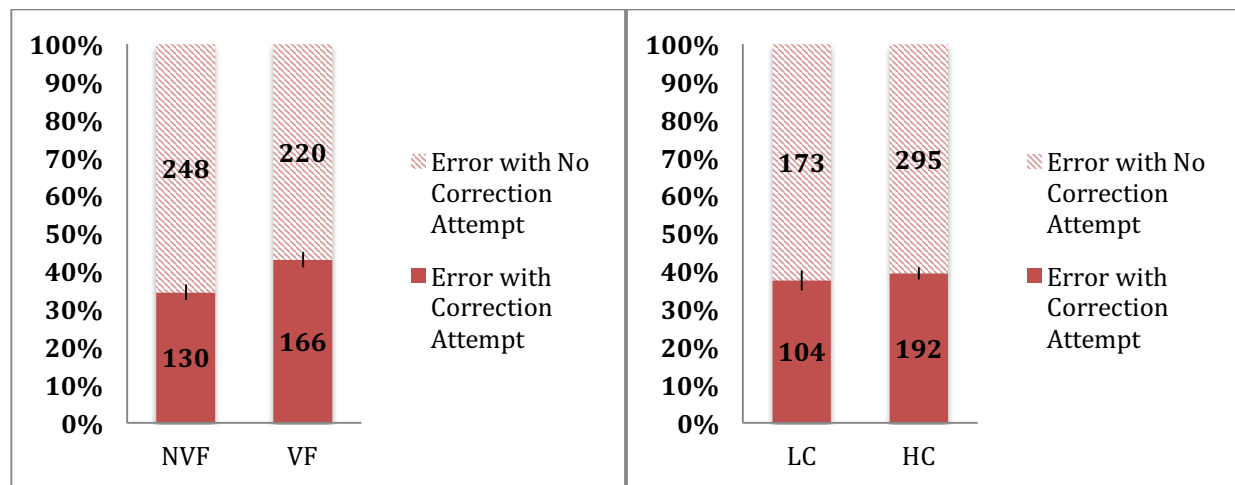|	Fixed Effects				Interaction
	Visual Feedback	Conflict	Action comprehension	Action production	Action comprehension: Feedback
Error correction Attempts	$\chi^2=5.75$ $p=.02*$ Estimate=.40 SE= .17	$\chi^2=.71$ $p=.40$ Estimate=.15 SE= .17	$\chi^2=1.11$ $p=.29$ Estimate=3.69 SE= 3.44	$\chi^2=.52$ $p=.47$ Estimate=-.33 SE= .44	
Successful Error Correction	$\chi^2=13.18$ $p=.003**$ Estimate=1.03 SE= .29	$\chi^2=17.19$ $p<.001***$ Estimate=-1.24 SE= .31	$\chi^2=.41$ $p=.53$ Estimate=1.70 SE= 2.67	$\chi^2=0.71$ $p=.40$ Estimate=.30 SE= .36	$\chi^2=3.84$ $p= .048*$ Estimate=5.70 SE=2.88

Fig. 3. Counts of error trials in Experiment 2 that contained an error correction attempt versus no correction attempt displayed in terms of the factors visual feedback condition (LEFT) or conflict (RIGHT); note that left and right graphs *each* show 100% of error trials in the experiment. Correction attempts were more frequent with visual feedback (LEFT), but there was no effect of conflict (RIGHT). NVF = no visual feedback; VF = visual feedback; LC = low conflict, HC = high conflict.

4.2.2 Successful error correction

In the second statistical model we examined the probability of *successful error corrections;* in addition to main effects of conflict, visual feedback, action production, and action comprehension, we included the two-way interaction of action comprehension and visual feedback to test the prediction that successful correction with visual feedback would depend on the integrity of action comprehension.

As Table 5 and Figure 4 show, visual feedback substantially increased the likelihood of *successful error corrections.* S*uccessful error corrections* were less frequent for high conflict than low conflict items (See Figure 4). There was no effect of action production, nor was there a main effect of action comprehension. However, action comprehension significantly interacted with visual feedback (See figure 5). Likelihood ratio tests were performed to analyze the significant interaction. When visual feedback was available, action comprehension abilities tended to predict error correction, such that patients with better action comprehension tended to be more likely to correct their pantomime errors than patients with poorer action comprehension ($\chi 2$ (1)=2.89, p= .09). In contrast, without visual feedback, the probability of error correction was unrelated to the status of action comprehension ($\chi 2$ (1)= .05, p= .82).
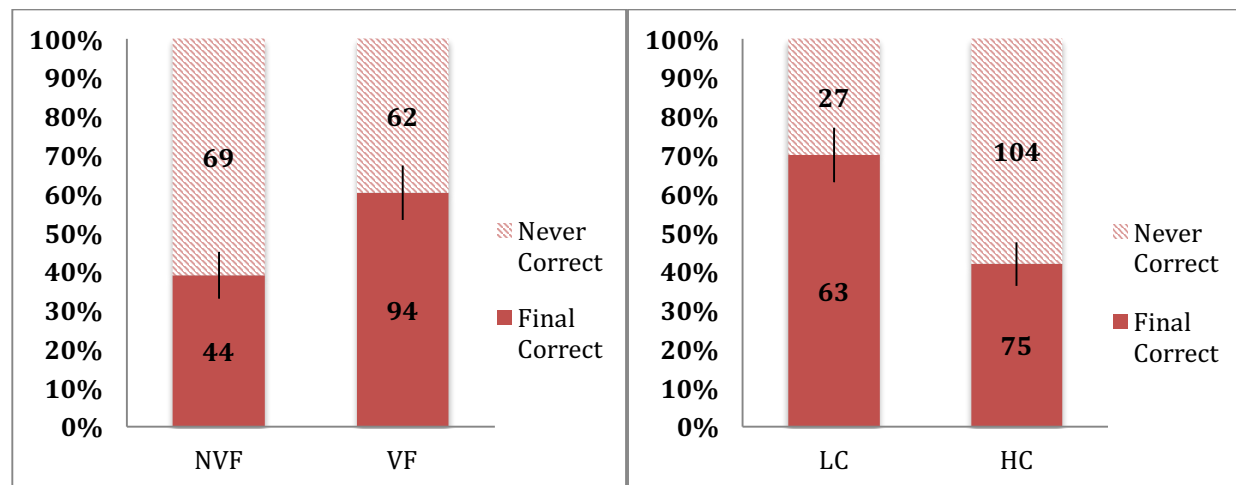

Fig. 4. Counts of error trials in Experiment 2 that were successfully corrected (Final Correct) versus those that contained only errors (Never Correct) displayed in terms of the factors visual feedback condition (LEFT) or (RIGHT); note that left and right graphs *each* show 100% of error trials. Final Correct trials were more frequent with visual feedback (LEFT) and with Low Conflict stimuli (RIGHT). NVF = no visual feedback; VF = visual feedback; LC = low conflict; HC = high conflict.
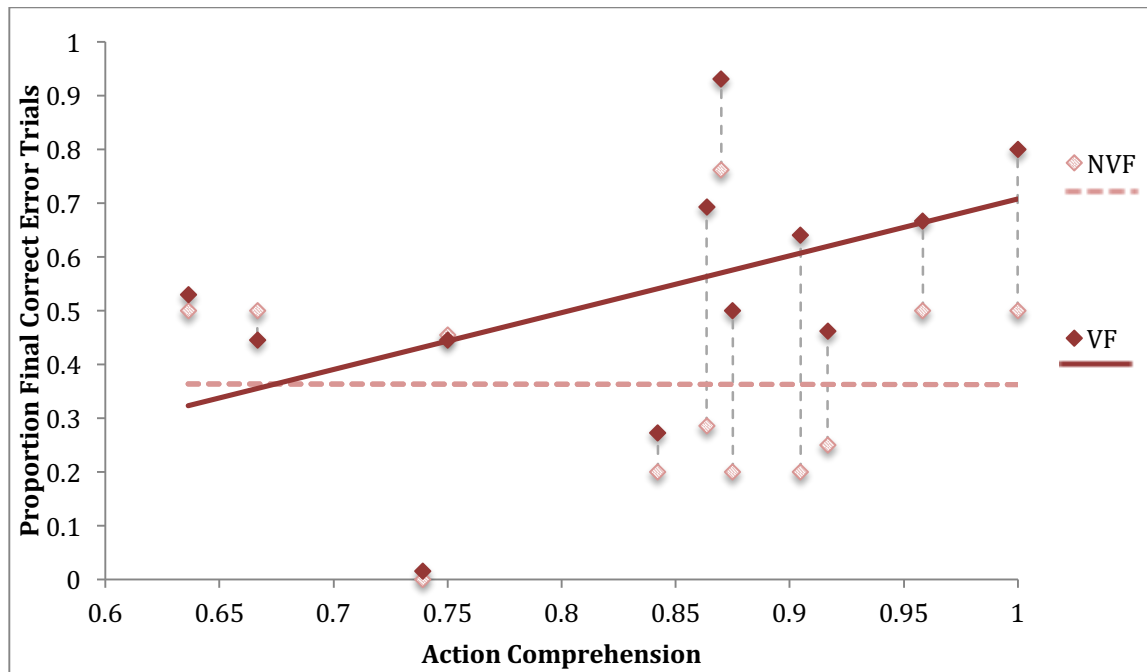
Fig. 5. Interaction of Action Comprehension and Visual Feedback. Proportion Final Correct error trials in the No Visual Feedback (NVF) and Visual Feedback (VF) conditions (Y axis) plotted against Action Comprehension scores (X axis). Two data points from each subject (one for the NVF condition and a second for the VF condition) are shown with connecting dotted grey lines. Note that there is no relationship between action comprehension and performance in the NVF condition. Critically, at higher levels of Action Comprehension, the benefit of VF (relative to NVF) is larger.

4.3 Discussion

Patients who produced moderate to severe CD showed two prominent patterns with respect to the role of visual feedback in error correction attempts and successful corrections. First, these patients strongly relied upon vision to monitor and repair their errors. Second, and most interestingly, vision tended to be helpful in correcting errors to the degree that action comprehension was intact. This pattern, suggestive of the comparison of a produced response and an internal representation of how the production should look, is consistent with use of an *external monitoring* strategy, as we will discuss further below. In contrast to the strong effect of vision, there was no evidence that the integrity of the gesture production system predicted correction attempts or successful corrections.

An unexpected but interesting difference emerged between the data from Experiments 1 and 2. In Experiment 1, there was a substantial effect of conflict on error correction attempts. In contrast, in Study 2 (with participants selected for moderate-severe CD), there was no effect of

conflict on error correction attempts. One interpretation of this difference is consistent with a qualified version of a *conflict monitoring* account in which we posit two routes to monitoring. Let us assume that in the healthy, undamaged system, response conflict (selection difficulty) provides a signal that extra response monitoring may be required. It follows that we may observe more error correction attempts with greater selection conflict (as predicted by that account) if patients are able to use normal internal predictive monitoring. However, consistent with the proposal of (Walker & Hickok, 2015), data from Experiment 2 suggests that patients with moderate-severe CD are overly reliant on visual feedback, and use their comprehension system to detect errors after they are committed. In patients using this external monitoring route, the presence of competition may be a less salient signal that monitoring and error correction are needed. Thus, conflict effects may be reduced in patients with moderate-Severe CD.

To assess this two-route hypothesis, we performed a post-hoc analysis on the data from Experiment 1. Patients in that larger sample were split into two groups based on whether the proportion of their trials that were error correction attempts was above or below the group median (median = .10). This resulted in a group of 33 patients with low error correction trials, i.e., no CD to moderate CD (M=.03) and a group of 34 patients with high error correction trials, i.e., moderate to severe CD (M=.25). We re-ran the statistical model with the error correction attempt data from Experiment 1, this time adding a fixed effect of group (low vs. high error correction trials) and an interaction term of group and conflict. The post-hoc likelihood ratio test revealed a significant two-way interaction of group and conflict ($\chi2$ (1) = 53.94, p=.003), OR = 5.11, 95% CI [2.01, 15.84]. Main effects of conflict were then tested for each group individually. As can be seen in Figure 6, the likelihood ratio tests showed a strong sensitivity to conflict in the low error correction group ($\chi2$= 22.26 *p*< .001), consistent with what we had seen earlier in the Experiment 1 group as a whole. In contrast, there was a reduced sensitivity to conflict in the high error correction group ($\chi2$=2.37 *p*= .12), consistent with the pattern seen in the Experiment 2 sample. Thus, only patients with little or no CD produced increased error correction attempts in the presence of response conflict. Importantly, although the overall rate of total errors in the task (an index of apraxia severity) was higher for the high than low error correction group, $t_{(66)}$ = 2.87, p = .003, a follow up model confirmed that the interaction between group and conflict remained significant when we controlled for total accuracy ($\chi2$ (1) = 13.04 *p*=.003).
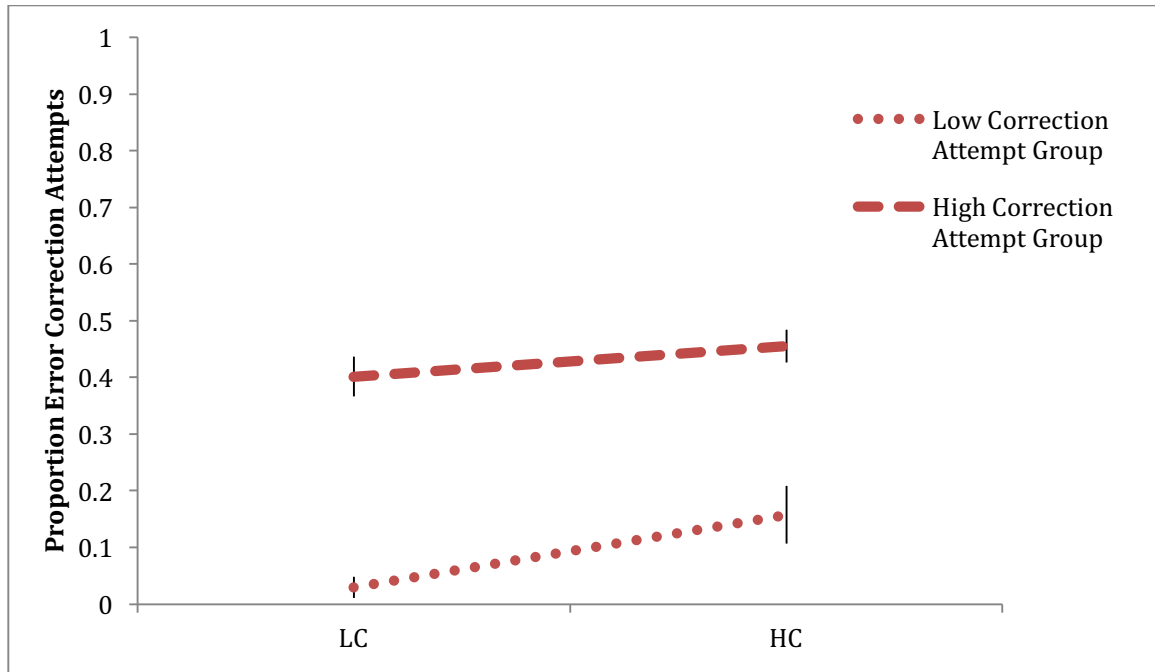
Fig. 6. Influence of action competition on proportion of error correction attempts in patients with high numbers of error correction trials (dashed line) and few or no error correction trials (dotted line). The effect of conflict was significantly more pronounced in patients who made few or no multiple responses. LC = low conflict condition; HC = high conflict condition.

5. **General Discussion**

Capitalizing on the fact that complex action in limb apraxia may be associated with conduite d'approche— a behavior that has been fertile ground for studying monitoring in language—we derived several competing predictions from the language domain to assess the mechanisms and neuroanatomical substrates of monitoring and correction of errors in complex limb actions in left hemisphere stroke. In line with *conflict-based* monitoring accounts, we showed that patients with little to no CD in action are more likely to detect and attempt to correct their errors when stimuli evoke competition. In contrast, consistent with *external monitoring* accounts (and inconsistent with both production-based and conflict-based *internal monitoring* accounts), error detection in patients with moderate to severe CD is not influenced by response competition or the integrity of the action production system. Instead, these patients attempt to rely on the action comprehension system in conjunction with online visual feedback to correct errors, and their ultimate success tends to be a function of the integrity of comprehension.

The observed differences in the factors influencing performance in patients with little to no CD (whose error correction attempts are sensitive to conflict) versus those with moderate-

severe CD (insensitive to conflict, but reliant on visual feedback and action comprehension) is consistent with two distinct routes to monitoring action errors. We suggest that patients with little to no CD are able to detect unfolding errors early in production, using competition as a signal that additional monitoring and cognitive control are required. The data indicating that patients who produced less CD also produce fewer errors, overall, are consistent with the possibility that such monitoring may help to reduce errors.

At which processing stage(s) might competition serve this role? Many production-based accounts of speech monitoring (e.g., Tourville & Guenther, 2011; Kroger, Crawford, Bekolay, & Eliasmith, 2016) suggest that motor planning of articulatory utterances generates an "efference copy" that can be monitored to rapidly detect the match between predicted sensory feedback and target sensory states. However, it is unclear whether competition monitoring (more specifically) arises during motor planning, per se. Although earlier accounts posit that conflict at the *response* level serves as a signal that monitoring is required (e.g., Botvinick, Cohen, & Carter, 2004), recent studies of reaching to targets in the motor control literature suggest that it is unlikely that two motor plans are concurrently selected such that they are co-activated and compete with one another (e.g., Wong, Haith, & Krakauer, 2014). Instead, competition between potential actions appears to arise during an earlier, more abstract processing stage (Lee, Middleton, Mirman, Kalenine, & Buxbaum, 2013). Actions have a characteristic trajectory in space over time, whether (for example) performed by one limb, the other limb, or a leg. This observation is frequently cited as evidence that there is an abstract level of representation of action that is not specified with respect to the muscles (Albert & Ivry, 2009). This abstract representation may be akin to what Liepmann (1905) described as the "time-space-form picture of the movement"—a classic description of the representation that, when damaged, causes apraxia. We may speculate that competition at this abstract level may serve as a signal to the healthy action planning system that additional monitoring is required. Likely relevant is previous research showing that implicit competition between actions associated with tools normally influences performance on word-picture matching (Watson & Buxbaum, 2014) and eyetracking (Lee et al., 2013) tasks, and that this competition is abnormally reduced and delayed in some apraxic patients (Lee, Mirman, & Buxbaum, 2014; Myung et al., 2010).

In patients for whom the internal predictive route is damaged, error monitoring must proceed via a second, slower external route in which patients' productions are successively

visually checked against memories of what actions 'should' look like. This route is successful only to the degree that action comprehension (which, in turn, requires visual memory of the characteristic appearance of actions) is intact. This account is similar to the Walker and Hickok (2015) view of conduite d'approche in language as resulting from the routing of auditory input through (intact) semantics and then on to lexical access when the predictive auditory-motor system fails. It is also similar to an account proposed by Ueno and Lambon Ralph (2013), who suggest that deficient phonological output is compensated by lexical-semantic "clean up" in patients for whom lexical-semantic processing is intact.

Although the similarities between CD in action and language appear clear, there are also several differences. One difference concerns the time course of our ability to respond to visual as compared to auditory feedback as it implicates the workings of the slower, non-predictive route. That is, latency differences in low level responses to visual or auditory information has implications for the rapidity with which language or action comprehension systems can access the patient's own motor system to correct errors on-line, as is proposed in the case of *external monitoring* accounts. Responses to visual input in primary visual cortices are generally slower (50-60 ms.; Foxe & Simpson, 2002) than responses in primary auditory cortices (20-50 ms; (Woldorff et al., 1993). Moreover, the observed differences in auditory versus visual latencies may extend to online sensory-based correction. In paradigms in which participants point to a target that jumps to another point within reaching distance on a portion of trials, reaching path correction range from 145 to 174 ms (Prablanc and Martin (1992)). In similar studies with "auditory perturbations" of certain formant frequencies in participants' own speech, compensation latencies are approximately 136 ms (Tourville, Reilly, & Guenther, 2008). Responses to similar perturbations of pitch can occur even more rapidly, as early as 100 ms (Xu, Larson, Bauer, & Hain, 2004). Given that auditory and visual feedback signal the need for correction in the language or action comprehension system, respectively, these data suggest that the signal of a 'mismatch' between produced sounds or actions and target sensory states may be more rapidly accessible in the auditory system as compared to the visual system. An open question is whether these posited differences in latency influence the success of correction efforts in the language versus action domain.

Both somatosensation and proprioception are also likely to play a role in error detection in both the speech and action domains, but perhaps to differing degrees. Proprioception is

critically important for the online control of limb movements (e.g., Goodman & Tremblay, 2018), whereas somatosensation is particularly critical for providing feedback on movements of the articulators (Nasir & Ostry, 2006). In action performed by neurotypical individuals, proprioception signals movement errors even when the effector is not in view. As noted above, in typing tasks somatosensory and proprioceptive signals allow for rapid error correction outside of conscious awareness. In parallel with the typing literature, we propose that the internal route in complex limb actions relies heavily on somatosensory and proprioceptive feedback. If the ability to integrate these forms of feedback with motor planning processes is disrupted, the external, visually-dependent route must be relied upon instead. Action conduite d'approche is a hallmark of this over-reliance on the external route.

A limitation of the present behavioral data is that we observed an unexpected differential sensitivity to conflict across experiments, such that sensitivity to conflict in the low CD group, versus sensitivity to visual input and action comprehension (but not conflict) in the high CD group was observed in a post-hoc analysis. Additional studies will be invaluable in testing the prediction of a more complete dissociation of the pattern in the two groups; specifically, that the low CD group should be minimally impacted by removal of visual feedback.

Examination of the neuroanatomic substrates of action CD with support vector regression lesion symptom mapping revealed areas of overlap between the regions implicated in speech error monitoring and those critical to complex action monitoring, as well as some differences. Lesions to several peri-sylvian cortical regions, including STG and AG (together, overlapping but extending beyond a region constituting the TPJ), Rolandic (parietal) operculum, MOG, SMG, insula, and pre- and post-central gyri resulted in high rates of action CD. This locus is broadly consistent with (but extends) the observation that area spt, in the sylvian fissure at the temporal-parietal boundary, is critical in CD in language. Area spt is activated both during speech input processing and during covert speech production, and thus has both auditory and motor response properties (Humphries, Willard, Buchsbaum, & Hickok, 2001; Hickok, Buchsbaum, Humphries, & Muftuler, 2003), and it has been suggested that this region may subserve the ability of online sensory input to guide production of vocal tract actions (Hickok & Poeppel, 2004; Pa & Hickok, 2008). In the action domain, more anterior regions along the sylvian fissure are candidates for performing a similar role. In particular, SII, a region at the foot of the somatosensory cortex, has

been shown to be critical to proprioception and may play a role in sensory-motor integration necessary to the optimal working of the "inner loop" (Lorey et al., 2009).

Also demonstrating a relationship to the language data was our finding that CD was associated with lesions to the arcuate fasciculus/superior longitudinal fasciculus, a white matter tract whose largest fiber bundle, SLFII, connects inferior parietal lobe with ventrolateral and dorsomedial frontal areas (Petrides & Pandya, 1984, 2009). AF/SLF lesions have long been regarded to be a primary source of CD in language (Geschwind, 1965); classic accounts posited that this fiber pathway is critical in connecting regions subserving auditory comprehension and those critical for production (Kempler et al., 1988).

Finally, a very different pattern involving the IFG and basal ganglia emerged when we considered regions that, when lesioned, were associated with diminished error correction attempts. One possibility is that patients with such lesions are less likely to detect their action errors than are patients whose lesions spare these regions. Reduced error detection, in turn, may be the outcome of faulty intention (i.e., planning errors; classically characterized as "mistakes"; (Reason, 1990) or may reflect a failure to monitor and detect "slips" -- productions that differ from goals. With regard to the latter possibility, numerous accounts of error monitoring in the complex action domain propose that cognitive processing resources including executive function are necessary to detect the mismatch between actions and intentions (e.g., Hart, Giovannetti, Montgomery, & Schwartz, 1998). Consistent with this possibility, the prefrontal cortex (along with the basal ganglia) are frequently implicated in studies of error detection and correction (see Eisinger, Urdaneta, Foote, Okun, & Gunduz, 2018; Ullsperger, Danielmeier, & Jocham, 2014; Wessel & Aron, 2017). Moreover, a neurophysiological marker of error monitoring, the error negativity (Ne), is reduced in patients with IFG lesions (Ries, Xie, Haaland, Dronkers, & Knight, 2013). Together, these data suggest that the observed failure of patients to produce error correction attempts after IFG and basal ganglia lesions may be the result of monitoring failures rather than lack of knowledge of target actions. Supporting this account are previous data we have reported indicating that posterior regions (posterior temporal lobe and IPL) and not IFG are critical for action knowledge (Tarhan, Watson, & Buxbaum, 2015).

5.1 Conclusions

Data from two experiments are consistent with two routes to error monitoring in complex limb actions. We propose that the *internal* route, mediated primarily by perisylvian temporal and parietal regions along with the arcuate fasciculus/superior longitudinal fasciculus, enables relatively rapid detection and correction of errors based on a comparison of predicted somatosensory and proprioceptive feedback and *somatosensory/proprioceptive* goal states. When this route is operating efficiently, competition at a relatively abstract stage of action planning serves as a signal that additional monitoring is required. When this route is damaged *and* action comprehension is intact, an *external* route may be used in which productions are visually monitored and the action comprehension system used to gradually 'clean up' mismatches between produced actions and *visual* goal states (see Ueno & Lambon Ralph, 2013). The evidence that both language and action monitoring can proceed via two routes, and the observation of similarities in the neuroanatomic substrates of the internal routes across the two domains pave the way for exploration of how abnormalities in patterns of error monitoring and correction may be related in aphasia and limb apraxia.

Acknowledgments

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