Neural correlates of response selection involved during forced choice paradigms: a neuroimaging meta-analysis

Neuronale Korrelate der Antwortselektion in Wahlreaktionsparadigmen: eine Metaanalyse von bildgebenden Studien

MASTERARBEIT

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Abstract

The appropriate motor responses must be selected and executed in a given context to facilitate goal-directed behaviour. Here, we aimed to delineate the brain regions that are involved in the selection of motor responses via quantitative meta-analysis of pertinent neuroimaging studies. In particular, we investigated the core neural correlates involved during forced two-choice response selection paradigms. In total, our sample comprised 48 studies: 25 for forced two-choice response selection with two-motor response options and 23 studies for forced two-choice response selection with respond and not-respond options, including 2,988 subjects in 48 contrasts with 1,054 activation foci. Consistent convergence in both datasets has been seen in the bilateral fronto-parietal network, the brain regions that may form the core network subserving response selection in humans, including the pre-supplementary motor area (preSMA), precentral gyrus, superior parietal lobule, and subcortical structures—putamen and bilateral cerebellum VI. Whereas several regions were sensitive to specific task components, e.g., the lateral occipital cortex and occipital fusiform gyrus were selectively active, which are thought to be involved during more complex visual processing of stimuli. In general, the Response Selection construct with respect to both impressions (i.e., Two Motor Response and Respond and Not-respond) engaged the same neural network despite the difference in the number of possible motor response options. Here, we discussed the possible functional roles of various nodes of this network as well as implications of our findings for a theoretical account of response selection. In conclusion, the shortcomings of previous studies are considered, and suggestions for future research are provided.

Keywords: response selection, forced two-choice, (f)MRI, meta-analysis, activation likelihood estimation (ALE) algorithm

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Introduction

Selecting and executing the appropriate motor actions in a given context is necessary to facilitate goal-directed behaviour. Response selection is a central decision-making process that converts incoming perceptual information to goal-appropriate motor output (Pashler, 1984; Welford, 1952). One theoretical framework that explicitly explains the several steps involved in the decision-making process is sequential-sampling models. These models suggest that basic decision-making entails gathering information from the environment until a certain response criterion threshold (i.e., the extent of information required to select a response) has been achieved (Brown & Heathcote, 2008; Ratcliff & Smith, 2004; Smith & Ratcliff, 2004; Usher & McClelland, 2001). The option that first meets the response criterion threshold is selected and then executed. Whereas it is thought that the perceptual and motor stage processes operate in parallel, it has been suggested that the central response selection stage is capacity-limited—only capable of taking an action on one task at a given time. For this reason, paradigms such as the psychological refractory period (Pashler, 1984; Welford, 1952), dual-task (Dux, Ivanoff, Asplund, & Marois, 2006; Dux et al., 2009; Schumacher et al., 2001; Sigman & Dehaene, 2008), and high-response-load single-task tests are frequently used to study this sensory-motor translation stage, because these measures place high cognitive demands on the response selection system. While the circumstances vary amongst different paradigms, all of them call on subjects to encode sensory data and make a decision, whereas in two-task paradigms, subjects are required to make simple response selections for items that appear simultaneously or shortly after one another.

To not respond to the stimulus, on the other hand, is believed to be a heterogeneous construct that can be parsed into at least two types: suppression that is both task relevant and task irrelevant (Harnishfeger, 1995; Nigg, 2000). Successful suppression of distractor stimuli is often measured in tasks where task-irrelevant information requires being ignored, such as the Eriksen flanker task (Eriksen & Schultz, 1979) and Stroop task (Stroop, 1935). Task-relevant response suppression, however, is often measured in tasks such as the stop-signal (Lappin & Eriksen, 1966, Verbruggen & Logan, 2008) and go–no-go (Donders, 1969) paradigms, which require the withholding of task-relevant, prepotent response tendencies on a subset of trials. Successful withholding in the stop-signal task depends on the outcome of a race between independent "go" and "stop" processes, according to the well-known race model explanation (Logan & Cowan, 1984). Response withholding succeeds when the suppression process finishes the race before the go process, whereas withholding fails if the go process reaches the response threshold first.

Traditionally, response selection and not responding (response withholding) processes have been investigated separately, but increasing evidence is suggesting that these two processes may draw on a common resource (van Gaal, Ridderinkhof, Fahrenfort, Scholte, & Lamme, 2008; Mostofsky & Simmonds, 2008; Verbruggen, McLaren, & Chambers, 2014). For example, research using neuroimaging and transcranial magnetic stimulation (TMS) has demonstrated that the presupplementary motor area (Buch, Mars, Boorman, & Rushworth, 2010) and the mid-dorsolateral and ventrolateral prefrontal areas (Bunge, 2004; Duncan & Owen, 2000) are activated by tasks that involve the selection and withholding of responses. Verbruggen, Aron, Stevens, and Chambers (2010) showed that TMS of the right inferior frontal gyrus (IFG) was shown to affect performance on a dual task and a stop-signal task. This suggests that the IFG supports both response selection and withholding processes. Taken together, these findings indicate that not responding (response withholding) and response selection protocols might tap, at least in part, a common mechanism of action control.

There is evidence to support the idea that response selection and response withholding processes may partially overlap at the neural level, but it also suggests that response selection and response withholding tasks recruit distinct brain regions. In fact, neuroimaging studies have shown that the posterior lateral prefrontal cortex (pLPFC) of left hemisphere is more active during dual-task trials as compared to single-task trials, suggesting that this cortical region is involved in response selection (Dux et al., 2006, Dux et al., 2009, Jiang & Kanwisher, 2003, Miller & Cohen, 2001). Similarly, for both single and dual tasks, Filmer and colleagues demonstrated that transcranial direct current stimulation of the left pLPFC but not the right pLPFC interferes with response selection and the associated training effects (Filmer, Mattingley, & Dux, 2013; Filmer, Mattingley, Marois, & Dux, 2013). In contrast, the right inferior frontal gyrus (rIFG) seems to be critical for the successful suppression of an inappropriate motor response (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003), since it shows greater activity during successful as compared to failed not-to-respond trials (Aron, Robbins, & Poldrack, 2014). These studies suggest process-specific functional differences and support the notion that response selection, and not responding to the stimuli, produces distinct neural signatures, specifically that the left pLPFC is engaged in response selection and the right IFG is involved in suppression of inappropriate responses. These neural findings at least imply that these two processes could reflect distinct forms of action control, even though no study has directly evaluated whether these two processes can be fully dissociated in the brain.

The pre-supplementary motor area (preSMA) is considered one of the primary sites involved in voluntary action, where electrical stimulation is known to induce an urge to move (Fried et al., 1991). Whereas pre-SMA activity across multiple decisions necessary for voluntary actions is shown by fMRI meta-analyses, including deciding what action to take, when to take it, and whether to take it at all (Brass & Haggard, 2008; Zapparoli et al., 2017). The preSMA interacts with numerous cortical and subcortical regions (Nachev et al., 2008), providing a variety of possible networks as the neural substrate of awareness of action. Numerous neuroimaging studies (Farrer and Frith, 2002) have linked the insular cortex with the sense of control of actions, and its connections with the preSMA may also be critical for the experience of volition (Hallett, 2007). By means of its connections with premotor regions (Luppino et al., 1993), a premotor posterior parietal network that has been causally linked to the experience of conscious intentions to act may be influenced by the preSMA (Desmurget et al., 2009).

The cerebellar contribution to movement (Holmes, 1939) and cognition (Schmahmann and Pandya, 1997) has anatomical substrates that are provided by extensive connections between the cerebellum, spinal cord, and sensorimotor and association areas of the cerebral cortex. The cerebellum consists of ten lobules, congregated as the anterior lobule (lobules I through V), posterior lobule (lobules VI through IX), and the flocculonodular lobe (lobule X). Functional MRI (f)MRI studies in humans (Grodd et al., 2005) and physiological experiments in cats (Adrian, 1943; Snider and Eldred, 1951) reveal the presence of sensorimotor homunculi in lobules III–VI and lobule VIII. In contrast, association area projections (prefrontal, posterior parietal, superior temporal, posterior parahippocampal, and cingulate regions) are primarily localised to lobules VI and VII (Kelly and Strick, 2003; Stoodley and Schmahmann, 2010).

Studies on non-human primates and patients with brain damage/lesion have highlighted the role of the prefrontal cortex (PFC) in goal-directed behaviour (Milner, 1963; Fuster, 1980; Goldman-Rakic, 1987; Stuss and Benson, 1986; Owen et al., 1990). Achieving a goal necessitates the capacity to ignore distractions and suppress inappropriate responses, known as behavioural withholding to specific stimuli, while simultaneously keeping goal-relevant information in mind—a function referred to as working memory (Lurii͡A, 1966). However, the prefrontal cortex is strongly interconnected with the parietal cortex (Petrides and Pandya, 1984; Schwartz and Goldman-Rakic, 1984). When one area is temporarily deactivated by cooling, the response characteristics of neurones in the other area are altered. (Quintana et al., 1989; Chafee and Goldman-Rakic, 2000), suggesting close functional associations between the two regions. PFC and parietal cortex coactivation has been shown in brain imaging studies for a wide range of cognitive activities, such as those involving working memory (Friedman and Goldman Rakic, 1994, Jonides et al., 1998a, Cabeza and Nyberg, 2000) and behavioural withholding (Pardo et al., 1990, Sweeney et al., 1996, Garavan et al., 1999, Hazeltine et al., 2000).

The influence of top-down, covert attention on visually driven signals throughout the primate visual system has been the primary focus of research on visual selective attention, and this research has included parallel work in humans (Corbetta et al., 1991; Hillyard, 1993; Heinze et al., 1994; Luck et al., 2000; Pessoa et al., 2003) and non-human primates (Desimone, 1995; Reynolds & Chelazzi, 2004; Noudoost et al., 2010). The fundamental finding of the latter's neurophysiological investigations is that selective visual attention increases visually driven firing rates of the neurones encoding the attending stimulus; the dorsal lateral geniculate nucleus (dLGN) is the region where this modulation first appears (McAlonan et al., 2008), and this becomes more pronounced at later phases of visual processing (Moran & Desimone 2003, Luck et al., 1997, Maunsell & Cook 2002, Buffalo et al., 2009, Noudoost et al., 2010). These results from neurophysiological research (Kastner & Ungerleider 2001, Pessoa et al., 2003) are substantially supported by the findings of human functional brain imaging. Furthermore, these findings appear to be consistent for both feature/object-based and spatial attention (Treue & Martínez-Trujillo 1999, Sàenz et al., 2002).

Based on these anatomical projections and functional connectivity amongst these cortical and subcortical regions and networks, in this neuroimaging meta-analysis, we aimed to delineate the brain regions that are involved in the selection of motor responses via quantitative meta-analysis of pertinent neuroimaging studies. Where we have chosen basic forced two-choice response selection paradigm structures, i.e., Two Motor Response Options and Respond and Not Respond Options. Simon Task, Stimulus-Response Compatibility (SRC) Task, Stop Signal Task (SST), Anti-saccade Task, and Forced Choice Task were included in the paradigms selected for Two Motor Response Options. Whereas the n-Back Task and Go/No-Go Task (GNGT) were used for the Respond and Not Respond Options.

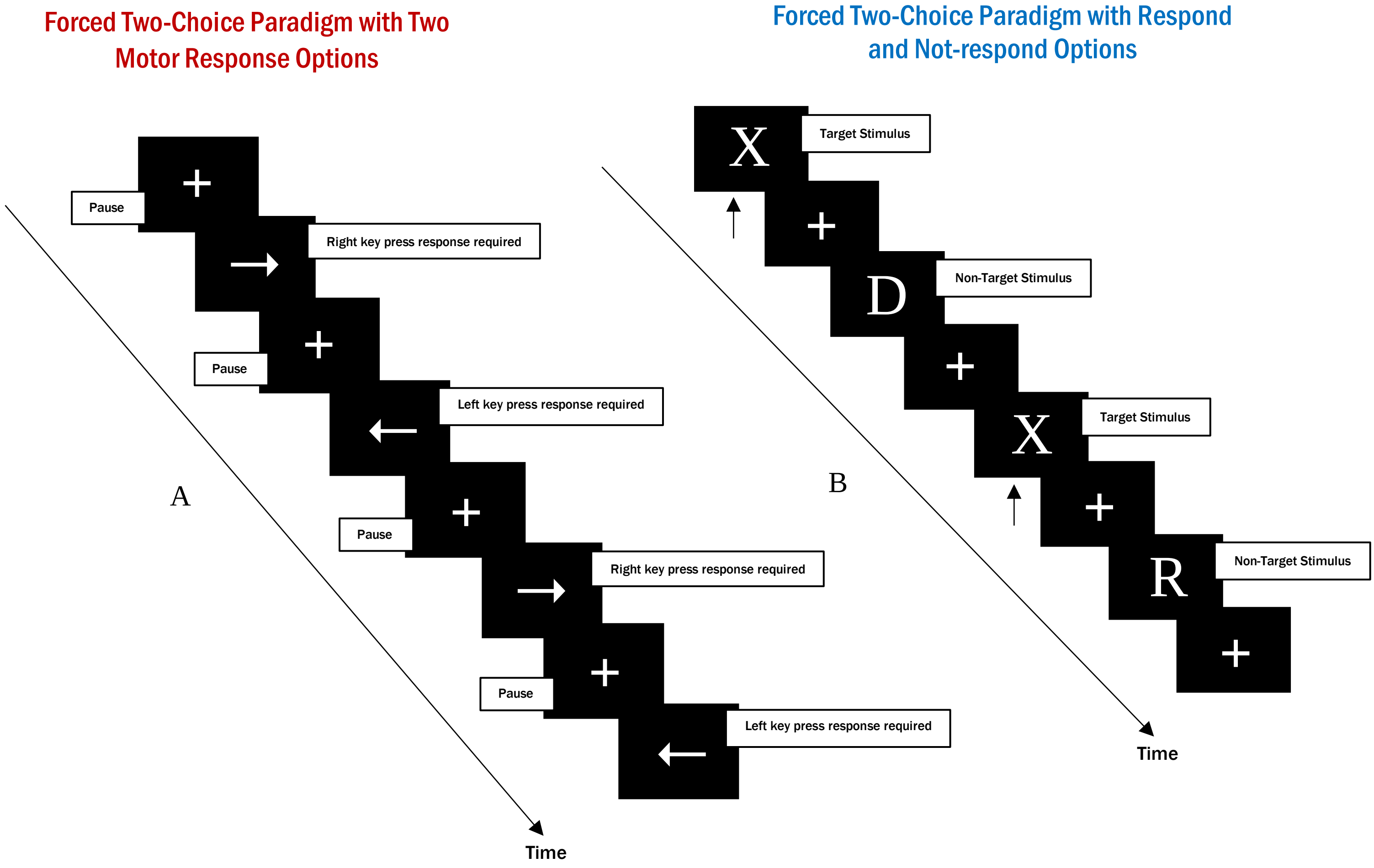
We tested which brain regions are consistently associated with both of these paradigm classes (i.e., Two Motor Response Options and Respond and Not Respond Options); we therefore performed a conjunction analysis across the thresholded ALE maps. Further, we aimed to reveal and compare those brain regions involved that are specific to either of these paradigm classes (i.e., when people responded to two motor compared to one motor response options) according to the presented stimulus.

Materials and Methodology

Inclusion criteria for Meta-analysis

A systematic approach was applied to identify the relevant experimental studies. For literature search we have used the search engines, e.g., PubMed (https://pubmed.ncbi.nlm.nih.gov/) and ScienceDirect (https://www.sciencedirect.com/) to scrutinise those publications that have used functional Magnetic Resonance Imaging (fMRI) or the Positron Emission Tomography (PET) imaging scans. In this meta-analytic study, we investigated neural underpinnings consistently involved during forced two-choice response selection. The key words that were used during the literature search include: “functional magnetic resonance imaging”/“fMRI,” “positron emission tomography”/“PET,” “neural correlates,” “Simon Task,” “Stop Signal Task,” “Forced Choice Task,” “Go/No-Go Task,” “n-Back Task,” “Stimulus-Response Compatibility Task”/“SRC Task,” and “Anti-saccade Task.” Furthermore, we also searched reviews and meta-analyses that used the forced two-choice experimental condition in their study.

Only studies that met the following criteria were included in this meta-analysis: studies reporting results from whole-brain group analysis as coordinates in standard reference space (Talairach/Tournoux or Montreal Neurological Institute [MNI]), whereas single-subject reports, results of Region-of-Interest (ROI) analysis, and studies not reporting standardised stereotactic coordinates were excluded. The data was extracted only from healthy individuals who were aged 18 years and above, while the results obtained from children and patients were excluded. In addition, in clinical studies, the data was extracted from only within-group effect from the healthy controls if separately reported or if the authors provided us with the necessary information upon request; data from conditions with pharmacological, “other” state manipulations (e.g., sleep deprivation or alcohol consumption) or non-invasive manipulations such as transcranial magnetic stimulation (TMS) was excluded. The control group receiving only a placebo intervention was excluded due to possible anticipation effects that might affect underlying neural responses, whereas results from normal control conditions without manipulation were included if separately available; the acquired data was pooled if the same participants participated in 2 or more experimental paradigms; only activation data resulting from subtractions between target conditions and control/resting baseline conditions were included; hence, we did not consider deactivation data. Furthermore, the authors (first author and/or principal investigator (PI) of the publication) were contacted if the given paper fulfilled the basic inclusion criteria for the meta-analysis, but they did not document the required contrast either in their paper or in supplementary data. Figure 1. shows the schematic representation of forced two-choice response selection, which involves two basic paradigm structures. Figure 1A illustrates the basic and general structure for the Forced Two-Choice Task with Two Motor Response Options. In such kinds of paradigms, subjects were instructed to press the right key when a rightward-pointing arrow was presented, or a left key press was required when a leftward-pointing arrow was displayed on the screen. Whereas Figure 1B shows the fundamental structure for the Forced Two-Choice Paradigm with Respond and Not Respond Options. Here, participants were instructed to respond to only the target stimulus (e.g., in Figure 1B, only the letter X was considered as a target stimulus, while all the other letters were the non-target ones). Based on the aforementioned criteria, 25 studies for Forced Two-Choice with Two Motor Response Options and 23 studies for Forced Two-Choice with Respond and Not-respond Options were identified as eligible for inclusion in the meta-analysis. Together, these studies reported 1,054 activation foci, acquired from 2,988 subjects in 48 contrasts.


Forced Two-Choice Paradigm with Two Motor Response Options

Forced Two-Choice Paradigm with Respond and Not-respond Options

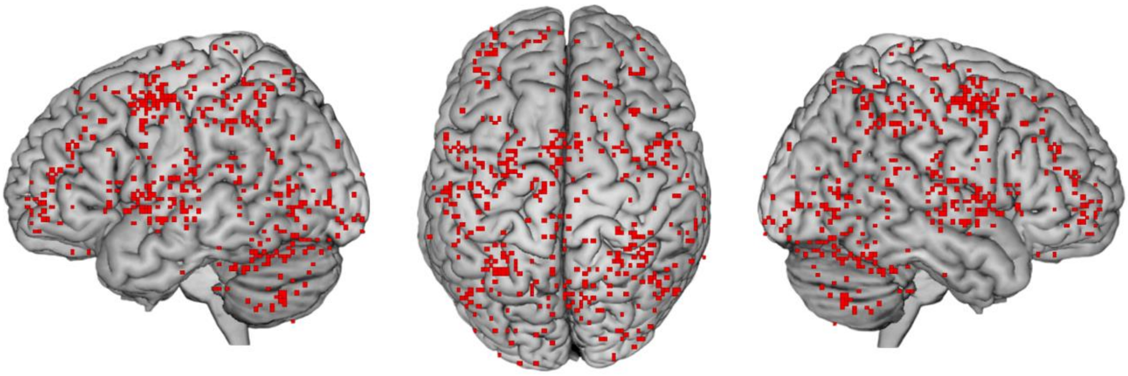
Fig.1: Schematic representation: (A). Forced Two-Choice Task with Two Motor Response Options and (B). Forced Two-Choice Paradigm with Respond and Not Respond Options.

Activation Likelihood Estimation (ALE) Algorithm

All meta-analyses were carried out with the revised version of the ALE algorithm designed for coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002). Analyses were performed in Python (version 3.12.4) (Frahm et al., 2022 https://github.com/LenFrahm/JALE). This algorithm is intended to identify brain areas where activity shows greater convergence across experiments than expected from a random spatial association. Reported coordinates are modelled as centres of three-dimensional Gaussian probability distributions, which represent the spatial uncertainty corresponding to each focus (Eickhoff et al., 2009). The between-subject variance is influenced by the number of subjects in each study, since large sample sizes contribute to more reliable approximations of the “true” activation effect and should therefore be modelled by “narrower” Gaussian distributions (Eickhoff et al., 2009). For each voxel, the probabilities of all foci documented in a given experiment were subsequently aggregated, resulting in a modelled activation map (Turkeltaub et al., 2012). Afterwards, voxel-wise ALE scores (i.e., the sum of all modelled activation maps) represent convergence across experiments at each particular location in the brain. To differentiate “true” convergence from random convergence (i.e., noise) across studies, ALE scores were compared to a null distribution that represents random spatial association across all the modelled activation maps. Rather than the clustering within a specific study, the random-effects inference yields above-chance convergence across experiments (Eickhoff et al., 2009). The null hypothesis was determined by calculating the distribution obtained when a voxel was randomly selected from each of the modelled activation maps and taking the union of these values, similarly performed (spatially contingent) for the voxels in original analysis (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2011a).

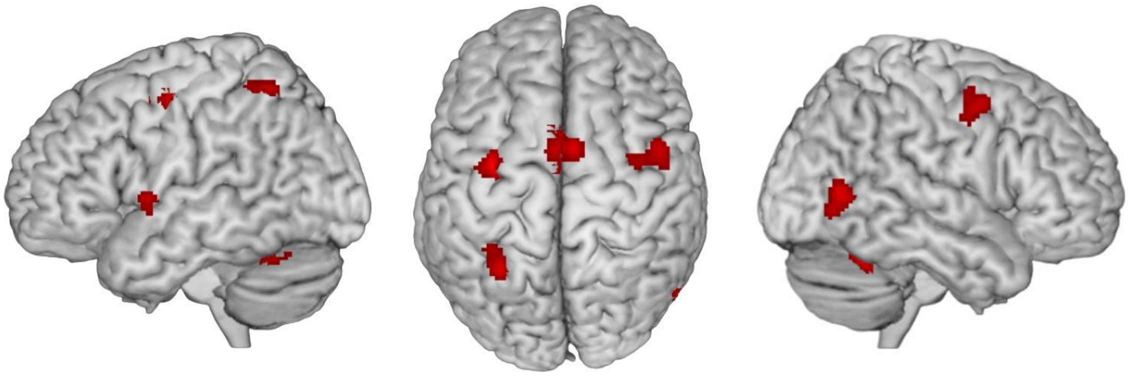
The results were corrected for multiple comparisons using cluster-wise family-wise error correction (cFWE). These corrections thresholds were estimated with an XGBoost forecast model used in the field of machine learning (ML). These XGBoost prediction models were formulated using Monte Carlo simulations (Chen and Guestrin, 2016; Frahm et al., in preparation). The proportion of values that were equal to or higher under the null distribution was used to calculate the p-value of a "true" ALE score. Next, the ALE maps showing convergence over experiments were thresholded at a cluster-level of $p < .05$ (cluster-forming threshold: $p < .001$ at voxel-level) (Eickhoff et al., 2012) and converted to Z-scores for visualization. A simulation study (Eickhoff et al., 2016) suggests that at least 17-20 experiments should be included in an Activation Likelihood Estimation (ALE) meta-analysis to have sufficient power to ensure that results are not influenced by individual experiments.

Further, if NIfTI-files contain a very large number of voxels within the clusters, then instead of taking just 10 sub-peaks from each cluster in the Statistical Parametric Mapping SPM12 Anatomy Toolbox (version 3.0), we have extracted the first 20 sub-peaks from each cluster via FSL (stands for FMRIB—**F**unctional Magnetic Resonance Imaging of the Brain **S**oftware **L**ibrary) `*cluster*` (version 6.0.3)—a comprehensive library of analysis applications used for (f)MRI, MRI, and Diffusion Tensor Imaging (DTI) brain imaging data.



Location of the individual activation foci as reported in the publications.

Reported coordinates in the publications are modelled as centres of three-dimensional Gaussian probability distributions.
Activation Likelihood Estimation reflecting for each voxel the union of the modelled activation (MA) maps across all experiments.



Then, the ALE maps that demonstrated convergence across experiments were then converted to Z-scores for visualisation after being thresholded at a cluster-level of $p < .05$ (cluster-forming threshold: $p < .001$ at voxel-level) (Eickhoff et al., 2012).

Fig. 2: The images illustrate various steps involved in the ALE Algorithm. Particularly, these images are extracted from the first database (i.e., the Forced Two-Choice paradigm with Two Motor Response Options) for the visualisation.

Description on Conjunction and Contrast Analysis

Conjunction analysis was used to determine which voxels showed a significant effect across two discrete analyses. To calculate the conjunction analyses between two ALE analyses, we employed the conservative minimum statistic (Nichols et al., 2005), which is equivalent to determining where the two cluster-level FWE-corrected results intersect (Caspers et al., 2010). In other words, only areas that were significant in both individual analyses at the corrected level were taken into account. A further cluster extend threshold of k ≥ 25 voxels was applied to exclude smaller regions of likely chance-level overlap between the thresholded ALE maps of the individual analyses.

To test for differences between datasets, separate ALE analyses were conducted for each data pool, and then the voxel-wise difference between the resulting ALE maps was computed (Eickhoff et al., 2011b). Following that, all of the experiments that went into either analysis were pooled and distributed into two groups at random, each of the same size as the two original sets of experiments reflecting the contrasted ALE analyses (Eickhoff et al., 2011a). ALE scores were computed for these two randomly distributed groups, and the difference between these ALE scores was logged for each voxel in the brain. Repeating this process 25,000 times then generated a null-distribution of differences in ALE scores between the two datasets. This voxel-wise null-distribution of label exchangeability was then used to assess the "true" difference in ALE scores, with a threshold set at $P > 0.95$ (95% chance for true difference). We inclusively masked the surviving voxels by the corresponding main effect, i.e., the significant effects of the ALE analysis for the specific condition (Langner and Eickhoff, 2013; Rottschy et al., 2012).

Furthermore, contrast analyses highlight regions where one of the two contrasted sets of experiments showed higher convergence; however, conjunction analyses show regions where two different effects (i.e., Two Motor Response Options and Respond and Not Respond Options) *both* indicate significant activation. Contrasting Two Motor Response Options with Respond and Not Respond Options unveils localities where there is a significantly stronger convergence amongst the former relative to the latter. However, this does not mean that the latter would not significantly converge. To put it another way, the convergence of activation sites reported for Respond and Not Respond Options may be similarly significantly greater than chance, even in locations where there is significantly stronger convergence of activation reported in Two Motor Response Options. In this case, both of the analyses that need to be contrasted would be significant independently. As a result, the conjunction and the contrast would both be significant at the very same location.

Therefore, if two sets of experiments converge strongly, but one set more than the other, contrast and conjunction effects may overlap rather than be mutually exclusive.

Anatomical Labelling

Reference to probabilistic cytoarchitectonic maps of the human brain (Eickhoff et al., 2005, 2007), the results were anatomically labelled using the Statistical Parametric Mapping SPM12 (Wellcome Department of Imaging Neuroscience, London, England) Anatomy Toolbox (version 3.0). As a result, activations were assigned to the most probable histologically defined region at each location. Each result table reports this histology-based anatomical labelling; the corresponding table notes contain references to specifics of the cytoarchitecture. The probabilistic Harvard-Oxford cortical structure atlas was used for the macroanatomical labelling of the regions that are not yet cytoarchitectonically mapped based on observer-independent histological examination—rather than providing purportedly histological labels derived from volume approximations of the (schematic) Brodmann atlas. Whereas MRIcron (version 1.0.2) software was used to generate the neuroanatomical images.

Table.1: Overview of all publications included in this coordinate based meta-analysis of Response Selection.

Paper	Subjects	Contrast	Stimulus Characteristics	% Targets	% Non-Targets	Nature of Task (Manual/Eye Movements)
Eickhoff et al., 2011	20	Response Selection > Baseline	Arrow	100%	-	Manual
Cieslik et al., 2015	18	Congruent > Baseline	Red Dot	100%	-	Manual
Jakobs et al., 2009	26	Response Selection > Control	Arrow	100%	-	Manual
Montojo et al., 2013	30	Go > Baseline	Arrow	Information not available	Information not available	Manual
Aron and Poldrack (2006)	13	Go - Null	Arrow	75%	25%	Manual
Rodriguez-Pujadas et al., 2014	33	Go > Baseline	Letter	75%	25%	Manual
Maguire et al., 2003	6	Go > Baseline	Colour	50%	50%	Manual
Chevrier et al., 2007	14	Go > Baseline	Letter	67%	33%	Manual
Jarvstad et al., 2019	24	Response Selection > Baseline	Grey Disc	Information not available	Information not available	Manual
Georgiou-Karistianis et al., 2012	14	Congruent > Baseline	Arrow	100%	-	Manual
Kawashima et al., 1996	9	Response Selection > Control	Colour	Information not available	Information not available	Manual
*Kenner et al., 2010	24	Correct Go > Baseline	Letter	75%	25%	Manual
*Sebastian et al., 2013	21	Congruent > Baseline	Arrow	75%	25%	Manual
*Ghahremani et al., 2012	18	Go > Baseline	Arrow	75%	25%	Manual
*Elton et al., 2023	144	Go > Baseline	Arrow	75%	25%	Manual
*Ceceli et al., 2023	24	Go Success > Baseline	Arrow	75%	25%	Manual
*Damiani et al., 2024	107	Go > Baseline	Arrow	75%	25%	Manual
*Loayza et al., 2022	23	Go > Idle	Arrow	60%	40%	Manual

Latz et al., 2019	266	Congruent > Baseline	Blue Dot	100%	-	Manual
*Cai and Leung (2009)	12	Go > Baseline	Bar	70%	30%	Manual
Aichert et al., 2011	56	Response Selection > Baseline	Green Dot	Information not available	Information not available	Eye Movements
Fukumoto-Motoshita et al., 2009	18	Response Selection > Baseline	Dot	Information not available	Information not available	Eye Movements
Herweg et al., 2014	22	Response Selection > Baseline	White Circle	Information not available	Information not available	Eye Movements
Matsuda et al., 2004	21	Response Selection > Baseline	Dot	Information not available	Information not available	Eye Movements
Jin et al., 2022	12	Response Selection > Baseline	White Disc	Information not available	Information not available	Eye Movements
Daamen et al., 2015	73	0-Back > Baseline	Letter	Information not available	Information not available	Manual
Fukuda et al., 2019	24	0-Back > Baseline	Number	14%	86%	Manual
Habel et al., 2007	47	0-Back > Baseline	Letter	37%	63%	Manual
Harding et al., 2016	34	0-Back > Baseline	Letter	29%	71%	Manual
Heinzel et al., 2016	29	0-Back > Baseline	Number	31%	69%	Manual
Kaminski et al., 2019	41	0-Back > Baseline	Number	14%	86%	Manual
King et al., 2015	17	0-Back > Baseline	Letter	33%	67%	Manual
Krug et al., 2008	85	0-Back > Baseline	Letter	37%	63%	Manual
Li et al., 2014	15	0-Back > Baseline	Letter	33%	67%	Manual
Li et al., 2019	24	0-Back > Baseline	Letter	33%	67%	Manual
Philip et al., 2016	13	0-Back > Baseline	Letter	33%	67%	Manual
Schlagenhauf et al., 2008	10	0-Back > Baseline	Number	14%	86%	Manual
Schneider et al., 2007	81	0-Back > Baseline	Letter	37%	63%	Manual
Smits et al., 2009	12	0-Back > Baseline	Number	Information not available	Information not available	Manual
Wu et al., 2017	45	0-Back > Baseline	Number	25%	75%	Manual
Verhallen et al., 2021	116	0-Back > Baseline	Letter	Information not available	Information not available	Manual
Takeuchi et al., 2018	1235	0-Back > Baseline	Letter	33%	67%	Manual
Pfefferbaum et al., 2001	10	0-Back > Baseline	Letter	31%	69%	Manual
Fedota et al., 2014	16	Go > Baseline	Letter	83%	17%	Manual
Liddle et al., 2001	16	Go > Baseline	Letter	50%	50%	Manual
Mostofsky et al., 2003	48	Go > Baseline	Colour	82%	18%	Manual
Watanabe et al., 2002	11	Go > Baseline	Colour	Information not available	Information not available	Manual
Baglio et al., 2011	11	Go > Baseline	Letter	80%	20%	Manual

Note: An asterisk represents that the data were provided by the authors upon request and were not explicitly mentioned in the paper.

Results

Meta-analysis for Two Motor Response Options

The meta-analysis of 25 experiments included in Two Motor Response Options revealed significant convergence in 9 distinct clusters (see Table.2 and Fig.3): the motor network, including presupplementary motor area (preSMA), extending into middle frontal gyrus (MFG), including pre-central gyrus as well. Moreover, convergent activity was found in the central opercular cortex, superior parietal lobule (SPL), and bilateral cerebellum—one of the subcortical structures involved in the movement execution. In addition, we have also observed the convergence in the left putamen and lateral occipital cortex (inferior division).

Table.2: Brain regions revealing significant convergence of activity related to the Forced Two-Choice Response Selection with Two Motor Response Options.

Macroanatomical Structure	L/R	x	y	z	Cytoarchitectonic Location[a]	z-score
Cluster 1 (598 voxels)						
preSMA	L	-6	4	48	Area 6mr/preSMA	5.69
preSMA	R	6	4	60	Area 6mr/preSMA	5.23
preSMA	L	-4	-2	52	Area 6mr/preSMA	4.89
preSMA	L	-4	4	60	Area 6mr/preSMA	4.74
preSMA	R	10	8	50	Area 6mr/preSMA	3.34
Cluster 2 (253 voxels)						
Precentral Gyrus	R	48	4	50		4.73
MFG	R	38	-2	50		3.93
Cluster 3 (221 voxels)						
Lateral Occipital Cortex, inferior division	R	50	-64	6	Area hOc5 [V5/MT]	5.29
Lateral Occipital Cortex, inferior division	R	48	-68	-2	Area hOc41a	4.35
Cluster 4 (208 voxels)						
Precentral Gyrus	L	-32	-4	50		6.08
Cluster 5 (151 voxels)						
Cerebellum Right VI	R	34	-54	-28		4.91
Cluster 6 (139 voxels)						
SPL	L	-30	-56	56	Area 7A (SPL)	5.1
SPL	L	-34	-46	58	Area 7PC (SPL)	3.73
Cluster 7 (131 voxels)						
Cerebellum Left VI	L	-34	-56	-28		4.47
Cerebellum Left VI	L	-28	-50	-26		3.52
Cerebellum Left (Crus I)	L	-38	-64	-24		3.23
Cluster 8 (103 voxels)						
Central Opercular Cortex	L	-50	4	2		4.53
Central Opercular Cortex	L	-56	4	-2		3.79
Cluster 9 (102 voxels)						
Putamen	L	-24	0	8		4.25
Putamen	L	-22	4	4		3.91

Note: Coordinates x, y, z of the cluster's peak voxel refers to Montreal Neurological Institute (MNI) space; Cytoarchitectonic Location indicates the major part(s) of each cluster. preSMA: preSupplementary Motor Area; MFG: Middle Frontal Gyrus; SPL: Superior Parietal Lobule. All activations exceed a threshold of $p < .05$ (cluster-level FWE-corrected). The x-coordinate goes from right to left (positive x is towards the right) side of the brain, the y-coordinate proceeds from anterior to posterior (positive y is anterior), and z-coordinate progresses from superior to inferior (positive z is superior) according to the anatomical orientation in the brain.

[a] References for histological assignments: Area 6mr/preSMA: Ruan et al. (2018); Area hOc5 [V5/MT]: Malikovic et al. (2006); Area hOc41a: Malikovic et al. (2016); Area 7A (SPL), Area 7PC (SPL): Scheperjans et al. (2008).

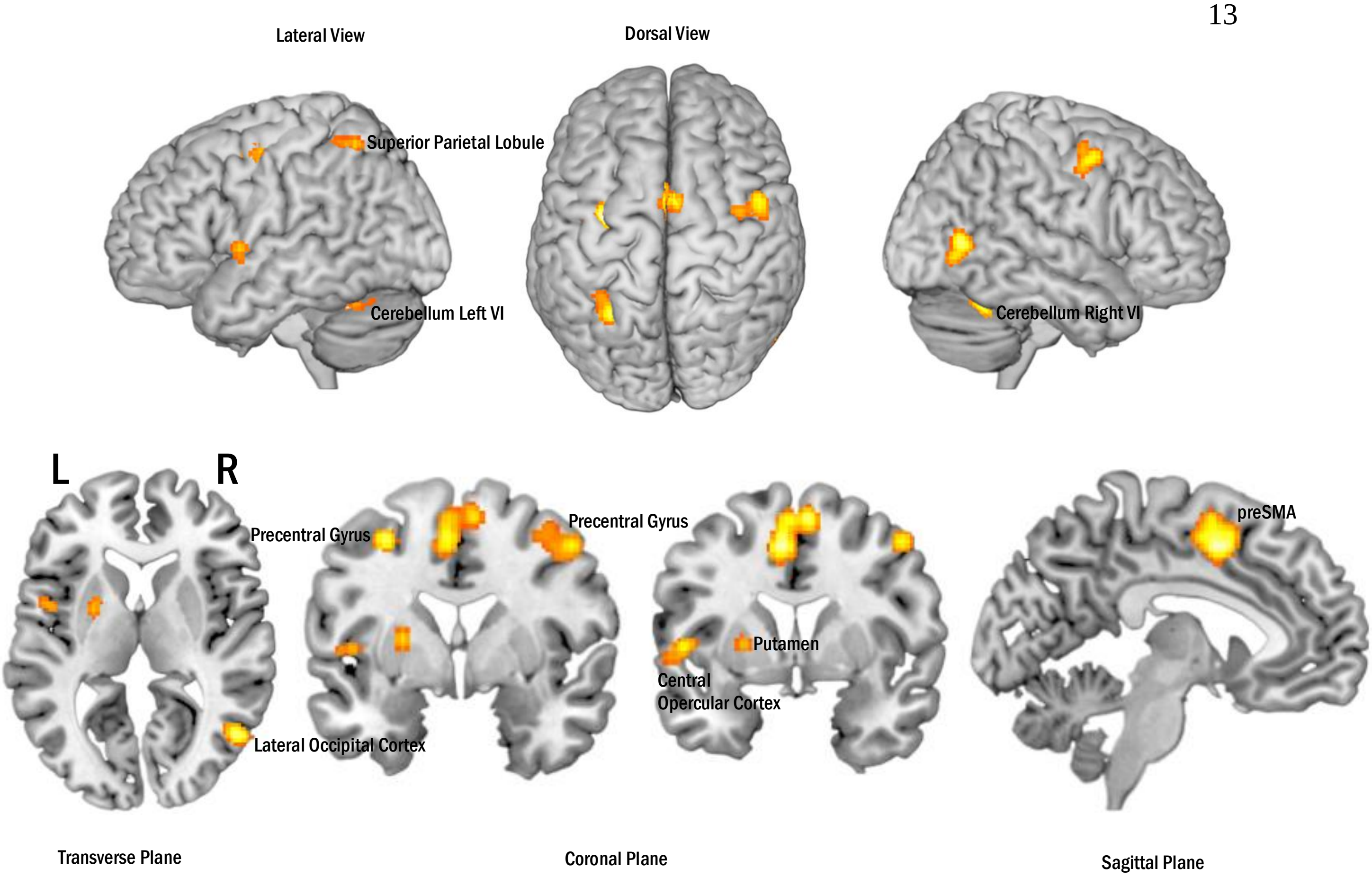


Fig. 3: Foci of brain activity with significant convergence across all 25 experiments included in the Forced Two-choice Response Selection with Two Motor Response Options meta-analysis (cluster level p < .05, family-wise error corrected for multiple comparisons; cluster-forming threshold p < .001 at voxel level. Brain sections display foci of significant convergence covered on the template brain with maps of cytoarchitectonically defined areas as included in the SPM Anatomy Toolbox 3.0 (Eickhoff et al., 2005). L indicates left hemisphere, whereas R denotes right hemisphere of the brain.

Meta-analysis for Respond and Not Respond Options

The meta-analysis of 23 experiments included in the Respond and Not Respond Options revealed significant convergence of increased activity in 12 clusters (see Table.3 and Fig.4): the motor network, including presupplementary motor area (preSMA), spreading into precentral gyrus. Convergence of activity has been seen in the left putamen, insular cortex, and bilateral cerebellum, whereas significant activation has been noticed in the lateral occipital cortex region and occipital fusiform gyrus as well.

Table.3: Brain regions showing significant convergence of activity related to the Forced Two-Choice Response Selection between Respond and Not Respond Options.

Macroanatomical Structure	L/R	x	y	z	Cytoarchitectonic Location[a]	z-score
Cluster 1 (668 voxels)						
preSMA	L	-6	2	54	Area 6mr/preSMA	7.81
preSMA	R	6	8	50	Area 6mr/preSMA	5.37
Cluster 2 (516 voxels)						

Lateral Occipital Cortex, inferior division	R	46	-70	-6	Area hOc41a	5.74
Lateral Occipital Cortex, inferior division	R	32	-90	0	Area hOc41p	5.18
Lateral Occipital Cortex, superior division	R	26	-88	6		4.77
Lateral Occipital Cortex, inferior division	R	42	-82	-4	Area hOc41a	4.28
Cluster 3 (516 voxels)						
Precentral Gyrus	L	-52	2	40		5.65
Precentral Gyrus	L	-46	-8	56		4.95
Precentral Gyrus	L	-38	-12	64		4.59
Precentral Gyrus	L	-38	-6	50		4.34
Cluster 4 (282 voxels)						
Insular Cortex	R	34	20	6		5.78
Central Opercular Cortex	R	46	6	2		4.33
Cluster 5 (265 voxels)						
Lateral Occipital Cortex, inferior division	L	-42	-74	-10	Area FG2	6.24
Cluster 6 (237 voxels)						
Cerebellum Right VI	R	26	-54	-26		5.49
Cerebellum Right VI	R	36	-46	-28		3.72
Cerebellum Right VI	R	34	-44	-28		3.72
Cluster 7 (200 voxels)						
Planum Temporale	R	62	-34	18		6.17
Cluster 8 (153 voxels)						
Putamen	L	-24	6	10		6.35
Putamen	L	-26	8	-2		3.54
Cluster 9 (134 voxels)						
Occipital Fusiform Gyrus	L	-26	-88	-6	Area hOc3v [V3v]	4.09
Occipital Pole	L	-26	-92	2	Area hOc41p	4.08
Cluster 10 (133 voxels)						
Cerebellum Left VI	L	-36	-56	-28		4.29
Cerebellum Left VI	L	-28	-56	-26		4.09
Cluster 11 (116 voxels)						
Cerebellum Vermis VI	R	2	-68	-14		4.26
Cerebellum Vermis VI	L	-4	-70	-14		3.85
Cerebellum Right VI	R	8	-74	-20		3.67
Cluster 12 (100 voxels)						
Precentral Gyrus	R	52	6	46		5.26
Precentral Gyrus	R	44	0	40		3.33
Precentral Gyrus	R	42	0	36		3.27

Note: Coordinates x, y, z of the cluster's peak voxel refers to Montreal Neurological Institute (MNI) space; Cytoarchitectonic Location indicates the major part(s) of each cluster. All activations exceed a threshold of $p < 0.05$ (cluster-level FWE-corrected). The x-coordinate goes from right to left (positive x is towards the right) side of the brain, the y-coordinate proceeds from anterior to posterior (positive y is anterior), and z-coordinate progresses from superior to inferior (positive z is superior) according to the anatomical orientation in the brain.

[a] References for histological assignments: Area 6mr/preSMA: Ruan et al. (2018); Area hOc41a, Area hOc41p: Malikovic et al. (2016); Area FG2: Caspers et al. (2013); Area hOc3v [V3v]: Rottschy et al. (2007).

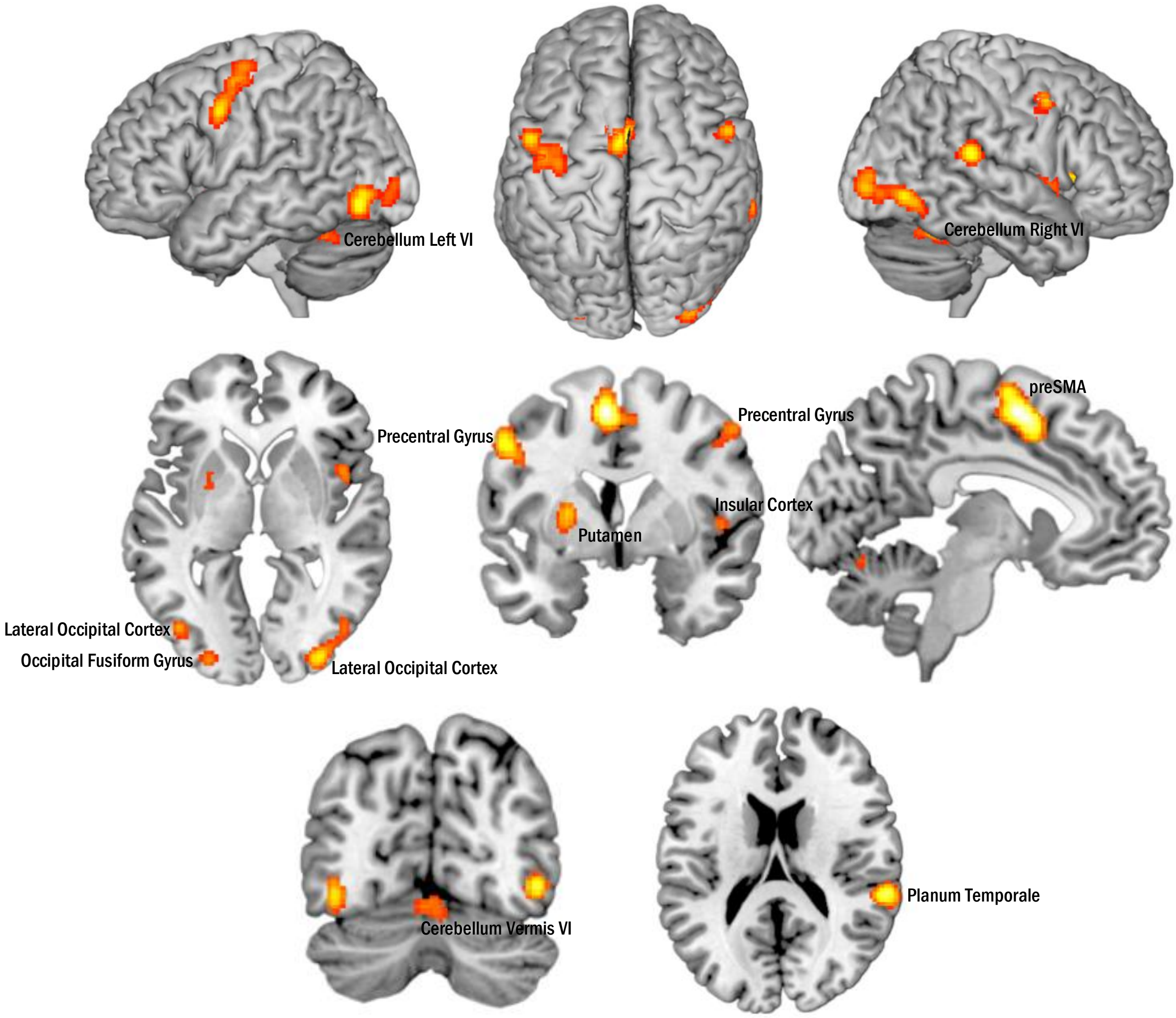


Fig. 4: Foci of brain activity with significant convergence across all 23 experiments included in the Forced Two-choice Response Selection between Respond and Not Respond Options meta-analysis (cluster level p < .05, family-wise error corrected for multiple comparisons; cluster-forming threshold p < .001 at voxel level. Brain sections show foci of significant convergence covered on the template brain with maps of cytoarchitectonically defined areas as included in the SPM Anatomy Toolbox 3.0 (Eickhoff et al., 2005).

Conjunction Analysis

To localise brain activity specifically related to Forced Two-Choice Response Selection, independent of the paradigms that have been chosen, we performed a minimum conjunction analysis across the thresholded ALE maps for both datasets (i.e., Two Motor Response Options, and Respond and Not Respond Options). This analysis revealed significant convergence in 6 clusters: preSMA, cerebellum (Ce) right and left VI, left putamen, precentral gyrus, and lateral occipital cortex (inferior division) (see Table.4 and Fig.5).

Table.4: The conjunction analysis revealing significant overlapping of anatomical regions.

Macroanatomical Structure	L/R	x	y	z	Cytoarchitectonic Location	z-score
Cluster 1 (372 voxels)						
preSMA	L	-6	6	48	Area 6mr/preSMA	5.67
preSMA	L	-4	-2	52	Area 6mr/preSMA	4.89
preSMA	L	-4	4	60	Area 6mr/preSMA	4.74
preSMA	R	6	4	54		3.43
preSMA	R	10	8	50	Area 6mr/preSMA	3.34
Cluster 2 (94 voxels)						
Cerebellum Right VI	R	32	-56	-26		4.61
Cluster 3 (88 voxels)						
Cerebellum Left VI	L	-34	-56	-28		4.25
Cluster 4 (49 voxels)						
Left Putamen	L	-24	2	8		3.94
Cluster 5 (37 voxels)						
Precentral Gyrus	L	-38	-6	50		4.34
Cluster 6 (29 voxels)						
Lateral Occipital Cortex, inferior division	R	48	-70	-2	Area hOc5 [V5/MT]	4.12

Note: Coordinates x, y, z of the cluster's peak voxel refers to Montreal Neurological Institute (MNI) space; Cytoarchitectonic Location indicates the major part(s) of each cluster. All activations exceed a threshold of $p < 0.05$ (cluster-level FWE-corrected). The x-coordinate goes from right to left (positive x is towards the right) side of the brain, the y-coordinate proceeds from anterior to posterior (positive y is anterior), and z-coordinate progresses from superior to inferior (positive z is superior) according to the anatomical orientation in the brain.

[a] References for histological assignments: Area 6mr/preSMA: Ruan et al. (2018); Area hOc5 [V5/MT]: Malikovic et al. (2006).

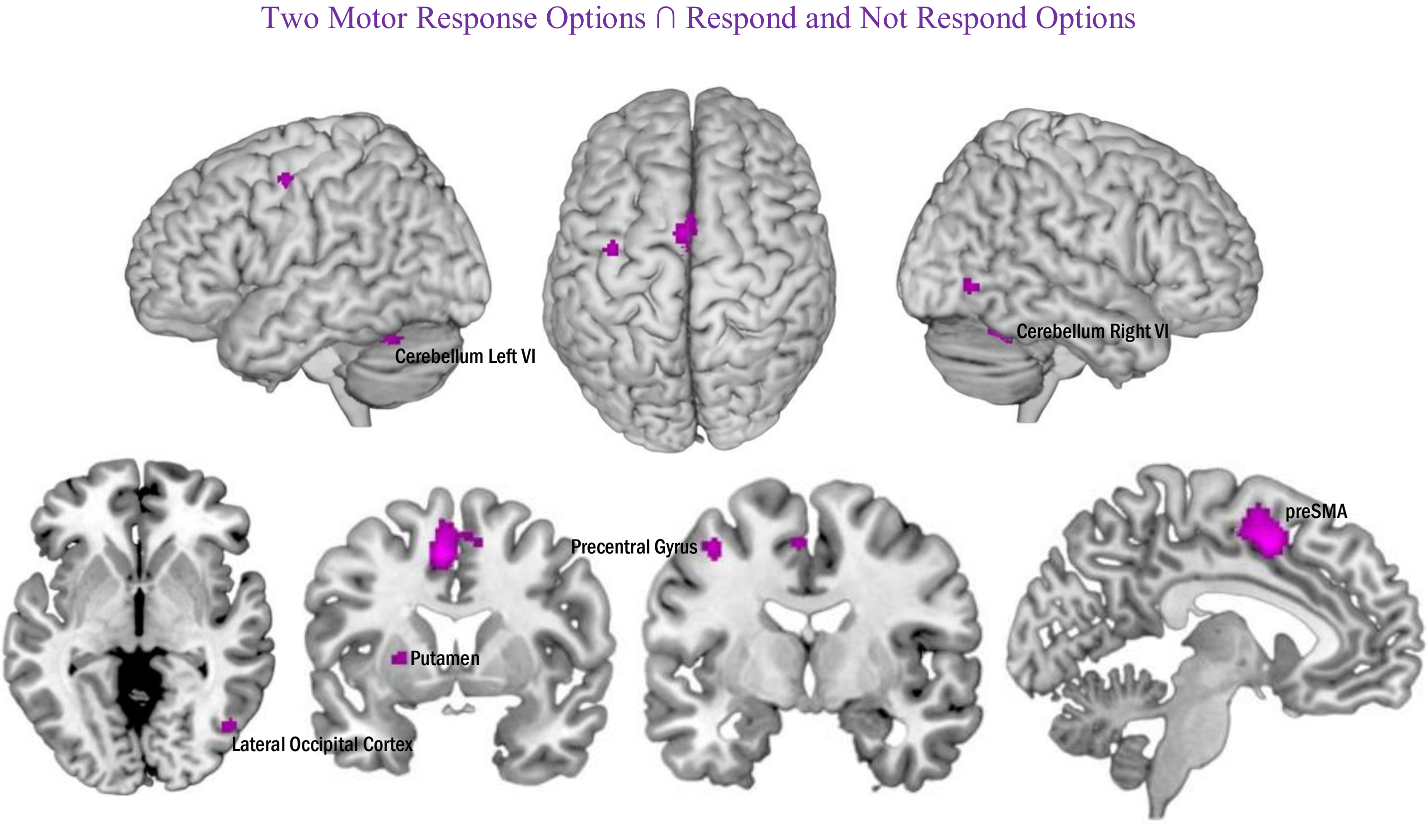

Two Motor Response Options ∩ Respond and Not Respond Options

Fig. 5: Performing a minimum conjunction analysis across both datasets (i.e., Two Motor Response Options, and Respond and Not Respond Options) revealed the preSMA, Cerebellum right and left VI, left Putamen, Precentral Gyrus, and Lateral Occipital Cortex, inferior division to be the only regions showing conjoint convergence of activity across both datasets.

Contrast Analysis

Each data pool underwent a separate ALE analysis to check for dataset differences, and then the voxel-wise difference between the resulting ALE maps was calculated. For Two Motor Response Options > Respond and Not Respond Options, the convergence of activity has been seen in 3 distinct clusters, including: lateral occipital cortex (inferior division), middle frontal gyrus, and superior parietal lobule. Whereas, Respond and Not Respond Options > Two Motor Response Options has shown the convergence in 10 significant clusters, which include: precentral gyrus, right lateral occipital cortex (inferior division), occipital pole, preSMA, parietal operculum cortex, frontal operculum cortex, occipital fusiform gyrus, left lateral occipital cortex (inferior division).

Table.5: The contrast analysis revealing significant convergence of activity related to the Two Motor Response Options > Respond and Not Respond Options.

Macroanatomical Structure	L/R	x	y	z	Cytoarchitectonic Location[a]	z-score
Cluster 1 (159 voxels)						
Lateral Occipital Cortex, inferior division	R	56	-64	8		3.24
Middle Temporal Gyrus, temporooccipital part	R	48	-60	8		3.24
Lateral Occipital Cortex, inferior division	R	54	-64	10		3.24
Lateral Occipital Cortex, inferior division	R	50	-62	10		3.24
Lateral Occipital Cortex, inferior division	R	48	-62	10		3.24
Middle Temporal Gyrus, temporooccipital part	R	52	-60	6		3.16
Lateral Occipital Cortex, inferior division	R	54	-66	4	Area hOc41a	3.04
Lateral Occipital Cortex, inferior division	R	52	-66	4	Area hOc5 [V5/MT]	3.04
Lateral Occipital Cortex, inferior division	R	52	-64	4	Area hOc5 [V5/MT]	3.04
Lateral Occipital Cortex, inferior division	R	52	-66	6	Area hOc5 [V5/MT]	3.04
Cluster 2 (103 voxels)						
Middle Frontal Gyrus	L	-28	-2	50	Area 6d3	3.16
Cluster 3 (100 voxels)						
Superior Parietal Lobule	L	-34	-44	56	Area 5L (SPL)	3.16
Superior Parietal Lobule	L	-30	-54	60	Area 7PC (SPL)	2.91
Superior Parietal Lobule	L	-30	-52	60	Area 7PC (SPL)	2.91
Superior Parietal Lobule	L	-30	-48	58	Area 7PC (SPL)	2.88
Superior Parietal Lobule	L	-32	-48	60	Area 7PC (SPL)	2.88

Note: Coordinates x, y, z of the cluster's peak voxel refers to Montreal Neurological Institute (MNI) space; Cytoarchitectonic Location indicates the major part(s) of each cluster. All activations exceed a threshold of $p < 0.05$ (cluster-level FWE-corrected). The x-coordinate goes from right to left (positive x is towards the right) side of the brain, the y-coordinate proceeds from anterior to posterior (positive y is anterior), and z-coordinate progresses from superior to inferior (positive z is superior) according to the anatomical orientation in the brain.

[a] References for histological assignments: Area hOc41a: Malikovic et al. (2016); Area hOc5 [V5/MT]: Malikovic et al. (2006); Area 5L (SPL), Area 7PC (SPL): Scheperjans et al. (2008a, 2008b).

Table.6: The contrast analysis revealing significant convergence of activity related to the Respond and Not Respond Options > Two Motor Response Options.

Macroanatomical Structure	L/R	x	y	z	Cytoarchitectonic Location[a]	z-score
Cluster 1 (176 voxels)						
Precentral Gyrus	L	-48	4	32		3.35
Precentral Gyrus	L	-54	2	34		3.24
Precentral Gyrus	L	-52	-2	44		2.31
Cluster 2 (160 voxels)						
Lateral Occipital Cortex, inferior division	L	-40	-80	-8	Area hOc41a	2.88
Occipital Fusiform Gyrus	L	-36	-74	-8		2.69
Lateral Occipital Cortex, inferior division	L	-38	-74	-8		2.69
Lateral Occipital Cortex, inferior division	L	-38	-74	-6		2.69
Lateral Occipital Cortex, inferior division	L	-40	-74	-6		2.69
Occipital Fusiform Gyrus	L	-42	-68	-14	Area FG2	1.83
Cluster 3 (99 voxels)						
Occipital Pole	R	32	-94	4	Area hOc41p	2.91
Occipital Pole	R	20	-90	8		1.98
Cluster 4 (87 voxels)						
Superior Frontal Gyrus	L	-10	-4	68	Area 6d1	2.08
preSMA	L	-2	4	54		1.96
preSMA	L	-4	4	54		1.96
preSMA	L	-6	2	56	Area 6mr/preSMA	1.95
Cluster 5 (80 voxels)						
Parietal Operculum Cortex	R	58	-30	20	Area PFcm (IPL)	2.77
Cluster 6 (76 voxels)						
Precentral Gyrus	L	-42	-8	64		2.49
Precentral Gyrus	L	-48	-12	58		1.86
Cluster 7 (65 voxels)						
Frontal Operculum Cortex	R	38	12	8		2.47
Cluster 8 (44 voxels)						
Occipital Fusiform Gyrus	L	-26	-84	-8	Area hOc4v [V4(v)]	2.73
Cluster 9 (28 voxels)						
Lateral Occipital Cortex, inferior division	R	46	-66	-12	Area FG2	2.12
Cluster 10 (26 voxels)						
Putamen	L	-28	10	14		2.6

Note: Coordinates x, y, z of the cluster's peak voxel refers to Montreal Neurological Institute (MNI) space; Cytoarchitectonic Location indicates the major part(s) of each cluster. All activations exceed a threshold of $p < 0.05$ (cluster-level FWE-corrected). The x-coordinate goes from right to left (positive x is towards the right) side of the brain, the y-coordinate proceeds from anterior to posterior (positive y is anterior), and z-coordinate progresses from superior to inferior (positive z is superior) according to the anatomical orientation in the brain.

[a] References for histological assignments: Area hOc41a: Malikovic et al. (2016); Area FG2: Caspers et al. (2013); Area hOc41p: Malikovic et al. (2016); Area 6mr/preSMA: Ruan et al. (2018); Area PFcm (IPL): Caspers et al. (2006, 2008); Area hOc4v [V4(v)]: Rottschy et al. (2007).

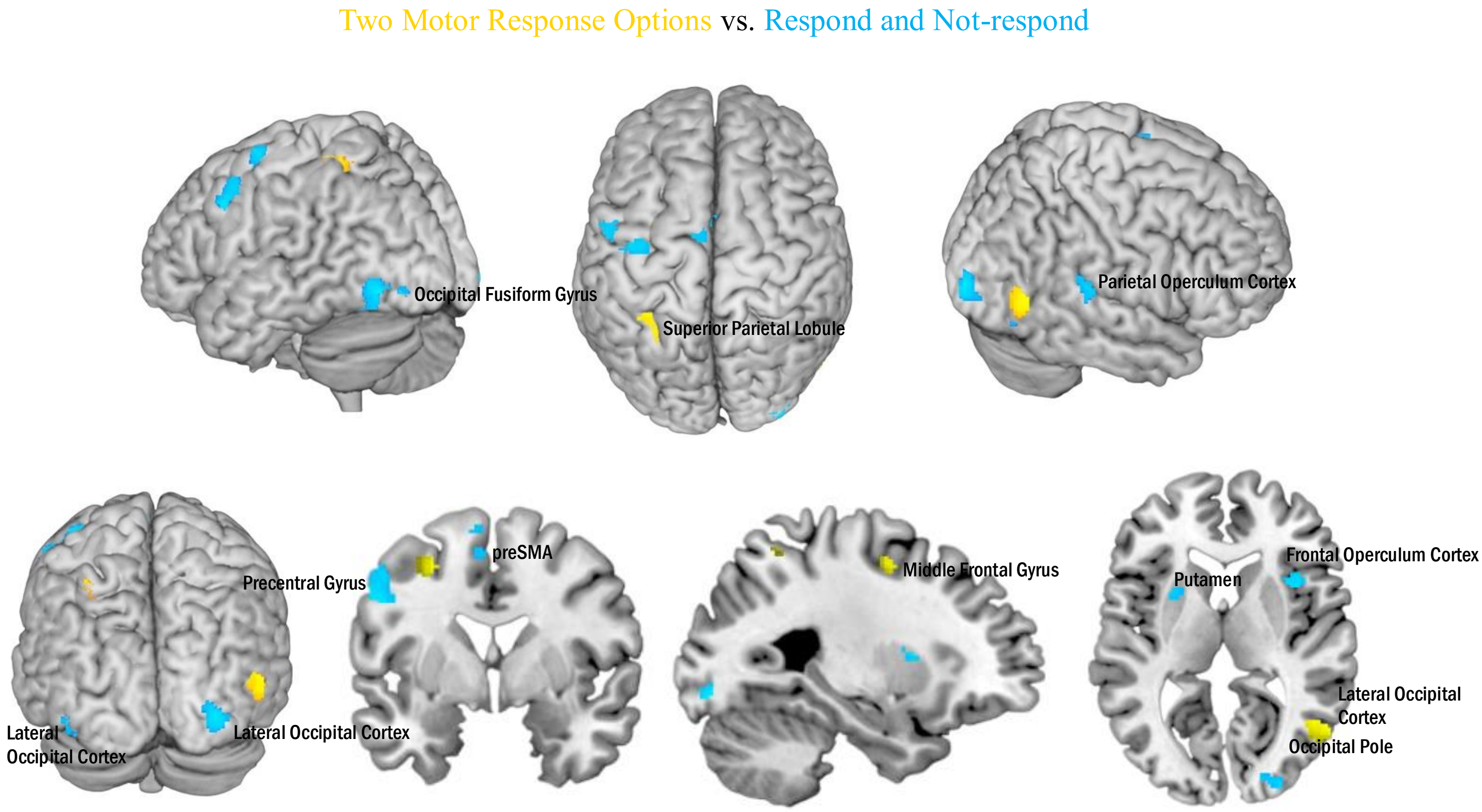


Fig. 6: Foci of brain activity with significantly stronger convergence in the Two Motor Response Options > Respond and Not Respond Options (yellow colour) and Respond and Not Respond Options > Two Motor Response Options (blue colour), respectively.

Discussion

We used coordinate-based ALE meta-analysis to analyse the neural correlates of response selection involved during forced two-choice paradigms. In total, 48 experiments were included for both of these databases, amongst which 25 studies were considered for two-motor response options, and 23 studies fulfilled the basic inclusion criteria for respond and not-respond options database. All the studies included in the Two Motor Response Options and Respond and Not Respond Options revealed a bilateral fronto-parietal network and subcortical regions, involving the preSMA, the precentral gyrus, the left putamen, the cerebellum right and left VI, and the right lateral occipital cortex (inferior division) are the regions that show consistent involvement in both datasets, as revealed by minimum conjunction analysis. Hence, we suggest that the preSMA, precentral gyrus, left putamen, cerebellum right and left VI, and the right lateral occipital cortex (inferior division) play a pivotal role in the processing of response selection. While other frontal, parietal, and sub-cortical regions were linked more specifically or were sensitive to individual task components.

Main Effect for Two Motor Response and Respond and Not Respond Options

For the paradigms that have been considered for two motor response options, significant convergence of activity has been found mainly in preSMA, precentral gyrus, lateral occipital cortex (inferior division), cerebellum right VI, superior parietal lobule, cerebellum left VI, central operculum cortex, and putamen (Fig.3). The pre-SMA is considered as the critical region for voluntary (Brass & Haggard, 2008) as well as involuntary actions (Flamez et al., 2021; Herz et al., 2015; Wolpe et al., 2014). Our results show bilateral convergence in the preSMA; however, the convergence is more dominant in the left preSMA. Potentially, this may be related to the fact that different studies included in the meta-analysis have varying manual requirements: some studies used right-handed selection tasks, whilst others used bimanual tasks. Further, previous fMRI studies have found that simple finger tapping movements activate contralateral putamen more than ipsilateral, whereas more complex movements may activate bilateral putamen (Reichenbach et al., 1998; Mattay and Weinberger, 1999). Neuropsychological studies have provided convergent evidence that the parietal cortex houses the response representations (Goodale and Milner, 1992). Ideomotor apraxia may be caused by damage to the parietal or prefrontal cortices, or to the connections between these two regions (particularly left lateralised); an inability to convert objectives into movements is a defining feature of this syndrome (Geschwind, 1975; Heilman et al., 1982). Apraxic patients who suffer from frontal and parietal damage both have difficulty executing appropriate motor movements. Moreover, parietal patients are impaired at imitating movements mentally (Sirigu et al., 1996) and unable to judge the movements of others (Kolb and Milner, 1981) and their own movements (Sirigu et al., 1999), suggesting that the parietal cortex plays a crucial role in encoding action-related knowledge. The lobules VI and VII, including the vermis of the lobules, are thought to be responsible for receiving input from the cerebral cortex (Dow, 1942; Ito, 1984). The lateral prefrontal cortex is functionally connected to the cerebellar regions in lobules VI and VII, according to neuroimaging studies that look at resting-state functional connectivity. (Habas et al., 2009). It has been proposed that lobules V, VI, and VII responded to the electrical stimulation to the forelimb representation in the monkey’s motor cortex (Sasaki et al., 1977). Finally, according to functional neuroimaging studies employing various cognitive tasks, it was revealed that the prefrontal cortex and cerebellar lobules VI and VII have shown activation by more cognitively demanding tasks. (Schmahmann, 2010; Stoodley and Schmahmann, 2009; Stoodley et al., 2012). Whereas the paradigms that are included in the respond and not respond options, the convergence of activity has been seen mainly in the preSMA, lateral occipital cortex (inferior division), insular cortex, precentral gyrus, putamen, planum temporale, occipital fusiform gyrus, cerebellum right VI, cerebellum left VI, and cerebellum vermis VI (Fig. 4). When there are multiple equally appropriate response options available for voluntary action decisions, the preSMA may resolve conflict between those options (Duque et al., 2013; Rushworth, 2008). It is widely acknowledged that attention speeds up the firing of neurones in specific visual regions. While the details of gain models differ in whether the increase can be better described as either multiplicative (Treue & Trujillo, 1999; Treue & Maunsell, 1999; McAdams & Maunsell, 1999) or as an increase in the effective strength of the stimulus (Reynolds et al., 2000), increased responses to both preferred and non-preferred stimuli are predicted by gain models. As the lateral occipital cortex is an area that is significant for processing object shape, according to the gain model, all of the neurones in the lateral occipital cortex that react to objects should respond more when attention is focused on them. The convergence of activity that we have seen in the bilateral occipital cortex can be argued and supported with these models and evidence findings. Whereas the parietal cortex and its projections to the dorsal and ventral premotor cortex are crucial for visuomotor processing, as evidenced by both human and non-human primate studies (Calton et al., 2002; Desmurget et al., 1999; Ellermann et al., 1998; Goodale and Milner, 1992; Hamzei et al., 2002; Jeannerod et al., 1995; Tanne-Gariepy et al., 2002) and predominantly in the reactive control of fine-tuned precision grip tasks (Dafotakis et al., 2008; Davare et al., 2007; Ehrsson et al., 2001; Haller et al., 2009). These regions work together to create parallel parieto-premotor circuits, which are responsible for transforming visual information into action (Rizzolatti et al., 1998; Wenderoth et al., 2006; Wise et al., 1997). The lateral visual regions obtain the pertinent spatiotemporal information of the feedback signal, whereas parietal regions make the essential sensory transformations for incorporating it with the required hand movements.

Conjunction Analysis

Conjunction analyses were performed to identify those brain regions that were consistently associated with the Two-Forced Choice Response Selection, with Two Motor Response Options AND Respond and Not Respond Options. This analysis showed us an overlap in the preSMA, Precentral Gyrus, Cerebellum right and left VI, left Putamen, and Lateral Occipital Cortex (inferior division). These results were consistent with previously identified motor network involved in response selection. Specifically, the recruitment of the primary motor cortex, and cerebellum is consistent with known motor maps seen in these structures (Buckner et al., 2011; Penfield and Rasmussen, 1950; Schlerf et al., 2010). Research on primates shows that the macaque homologue of PMv (ventral premotor area) has "mirror neurones," which are sensitive to both the observation and execution of actions. (di Pellegrino et al., 1992; Rizzolatti et al., 1996a; Gallese et al., 1996). Similarly, PMd (dorsal premotor area) has limited ability to directly contribute to movement execution (Dum and Strick, 2005); however, it has reciprocal connections with M1 and the spinal cord, which are associated more closely with action selection (Halsband et al., 1993; Rushworth et al., 1998). The preSMA has been associated with the production of voluntary action responses, whilst monitoring recent action history, or implementation of task strategies in a series of action decisions is similarly linked to the lateral prefrontal cortex (Cunnington et al., 2005; Hoffstaedter et al., 2013; Lau et al., 2004; Passingham et al., 2010; Rowe et al., 2000, 2010; Zhang et al., 2012).There are numerous potential explanations for common preSMA convergence during Two Motor Response Options and Respond and Not Respond Options. We suggested that a common cognitive process with a shared mechanism for Two Motor Response Options and Respond and Not Respond Options could be inhibitory in nature: for instance, Two Motor Response Options could include the inhibition of alternative actions or the suppression of previous actions in a series of action decisions (Rowe et al., 2010; Zhang et al., 2012), whilst Respond and Not Respond Options may necessitate the inhibition of an action currently in preparation (Aron and Poldrack, 2006).

Contrast Analysis

For the contrast analysis, we have compared both datasets (i.e., Two Motor Response Options and Respond and Not Respond Options) for the differences. When contrasting the Two Motor Response Option > Respond and Not Respond Options we have seen the convergence in the Lateral Occipital Cortex (inferior division), Middle Frontal Gyrus, and Superior Parietal Lobule (Fig. 6). Left parietal convergence has been seen for Congruent relative to Neutral trials, in addition to response code activation. The reason for this is that congruent stimuli involve more potentially relevant visual stimuli than neutral stimuli; hence, they may need more visuospatial attention. A substantial amount of data indicates that the right - and not left parietal cortex (around the angular gyrus) is crucial for visuospatial attention (Rushworth et al., 2001a,b). In contrast, attention to hand movements (Rushworth et al., 2001a,b) has been linked to a more anterior area of the left parietal cortex, which is close to a region that was active in the present study. When contrasting Respond and Not Respond Options > Two Motor Response Option, we have observed a broader fronto parieto-occipital regions that have shown convergence (Fig. 5). These regions have been linked to response selection, including selecting not to respond, stimulus recognition, and the maintenance and manipulation of stimulus-response associations. (Braver et al., 2001, Grafton et al., 1992, Law et al., 1997, Liddle et al, 2001, Mostofsky et al., 2003, Rubia et al., 2001 [illegible] Results from investigations on human lesions, electrophysiological, and functional neuroimaging support the key role of preSMA in the involvement of respond and not to respond to a stimulus. Single-cell recordings in monkeys have shown that an area similar to the pre-SMA is involved in not responding to a stimulus. (Matsuzaka et al., 1992). In humans, electrophysiological activity has been observed in the preSMA during suppression of responses (Ikeda et al., 1999), and direct stimulation of the preSMA region suppressed ongoing habitual motor actions (Ikeda et al., 1993). Lesions of the superior medial frontal lobe were linked to poor suppression of responses in the three largest human frontal lesion investigations (Drewe, 1975; Floden & Stuss, 2006; Picton et al., 2006). In fMRI studies of suppression of motor responses, pre-SMA activation has been a consistent finding (Bellgrove et al., 2004; Blasi et al., 2006; Braver et al., 2001; Rubia et al., 2001; Liddle et al., 2001; Fassbender et al., 2004; Kelly et al., 2004; Kiehl et al., 2000; Mostofsky et al., 2003).

Limitations

Since meta-analyses rely on the available empirical data, their findings may be affected by a publication bias in the literature that disfavours null results (R. G. Jennings & Van Horn, 2012; Rosenthal, 1979). Furthermore, as detailed elsewhere (Eickhoff & Bzdok, 2012; Rottschy et al., 2012), coordinate-based meta-analyses of neuroimaging data are less prone to publication bias than conventional meta-analytic methods that inspect effect sizes because the assessment of spatial convergence across experiments would not be affected by additionally including (observed but unpublished) null results. Therefore, we are certain that such bias did not significantly compromise the validity of our findings.

The data collected for the two datasets used in this study are heterogeneous in that different paradigms were included in the meta-analyses. Despite the fact, that only simple paradigms were taken into consideration and not the complex ones, the results indicate the involvement of other complex visual processing of stimuli. This may be because of the paradigms we used in the datasets (e.g., anti-saccade task, stop signal task, and/or n-Back task). Furthermore, the publications from the Stop Signal Task (SST) and n-back Task make up a substantial portion of our datasets; hence, the contributions from these studies might affect the results and may not always demonstrate specifically the response selection network in the brain. In addition, the contrasts we selected for both datasets were against resting baseline/control conditions, which were typically provided as secondary analysis or in supplementary data in most publications (especially in the newer ones) rather than as part of the primary analysis; as a result, this may also have an impact on the results. As the chosen contrasts were not the core component of the analysis explicitly published in their results section. Further, upon request, the data provided by (Schel et al., 2014) somewhat did not show any significant clusters of convergence; this might be the reason, because of the paradigm structure they employed in their experiment (i.e., the resting baseline condition was not well established to be contrasted).

Implications of the Study

The present study aimed to delineate the brain regions that are involved in the response selection via quantitative meta-analysis. Our results showed a bilateral fronto-parietal network with the involvement of sub-cortical regions. The study provides a pivotal role of preSMA, Cerebellum right and left VI, left Putamen, Precentral Gyrus, and Lateral Occipital Cortex (inferior division) in response selection, because these were the only regions consistently involved in both datasets as revealed by a minimum conjunction analysis. The results seem to be consistent with the previous findings in relation to the motor network in the brain. However, additional convergence outside the motor network within the occipital cortex might be better explained and argued with the specific paradigms selected. In conclusion, we can say that, by adopting a meta-analytic approach, it seems that the Response Selection construct with respect to both impressions (i.e., Two Motor Response and Respond and Not-respond) somehow engages the same neural network despite the difference in the number of possible motor response options. Due to the varying cognitive demand across all the paradigms included, future studies should take into account this aspect as well when investigating the neural substrates involved in the response selection construct concerning the involvement of number of possible motor response options.

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Note: References marked with an asterisk indicate studies included in the meta-analysis.

Appendix A. Experimental Contribution to the Particular Clusters

Forced Two-Choice Response Selection with Two Motor Response Options

25 experiments; 975 unique subjects (average of 39.0 per experiment)

Cluster 1: 598 voxels [Center: -2/4/54] Pre-supplementary Motor Area (PreSMA)	Cluster 2: 253 voxels [Center: 44/0/50] Precentral Gyrus	Cluster 3: 221 voxels [Center: 50/-66/4] Lateral Occipital Cortex, inferior division
1. Sebastian et al., 2013	1. Latz et al., 2019	1. Elton et al., 2023
2. Damiani et al., 2024	2. Jarvstad et al., 2019	2. Sebastian et al., 2013
3. Matsuda et al., 2004	3. Eickhoff et al., 2011	3. Cieslik et al., 2015
4. Georgiou-Karistianis et al., 2012	4. Sebastian et al., 2013	4. Eickhoff et al., 2011
5. Fukumoto-Motoshita et al., 2009	5. Aichert et al., 2011	5. Latz et al., 2019
6. Eickhoff et al., 2011	6. Kawashima et al., 1996	6. Montojo et al., 2013
7. Cai and Leung., 2009	7. Georgiou-Karistianis et al., 2012	7. Cai and Leung., 2009
8. Latz et al., 2019	8. Matsuda et al., 2004	8. Aichert et al., 2011
9. Aichert et al., 2011	9. Fukumoto-Motoshita et al., 2009	9. Maguire et al., 2003
10. Chevrier et al., 2007	10. Jakobs et al., 2009	10. Georgiou-Karistianis et al., 2012
11. Aron and Poldrack., 2006	11. Jin et al., 2022	
12. Maguire et al., 2003	12. Herweg et al., 2014	
13. Ghahremani et al., 2012		
14. Jarvstad et al., 2019		
15. Jakobs et al., 2009		
16. Montojo et al., 2013		
Cluster 4: 208 voxels [Center: -32/-4/50] Middle Frontal Gyrus	**Cluster 5: 151 voxels [Center: 32/-54/-26] Cerebellum Right VI**	**Cluster 6: 139 voxels [Center: -32/-54/56] Superior Parietal Lobule**
1. Chevrier et al., 2007	1. Latz et al., 2019	1. Ceceli et al., 2023
2. Latz et al., 2019	2. Georgiou-Karistianis et al., 2012	2. Matsuda et al., 2004
3. Aichert et al., 2011	3. Eickhoff et al., 2011	3. Fukumoto-Motoshita et al., 2009
4. Jakobs et al., 2009	4. Cieslik et al., 2015	4. Herweg et al., 2014
5. Eickhoff et al., 2011	5. Pastor et al., 2022	5. Eickhoff et al., 2011
6. Sebastian et al., 2013	6. Cai and Leung., 2009	6. Sebastian et al., 2013
7. Georgiou-Karistianis et al., 2012	7. Damiani et al., 2024	7. Jakobs et al., 2009
8. Cieslik et al., 2015	8. Ceceli et al., 2023	8. Aichert et al., 2011
9. Herweg et al., 2014	9. Ghahremani et al., 2012	9. Chevrier et al., 2007
10. Fukumoto-Motoshita et al., 2009	10. Elton et al., 2023	10. Cai and Leung., 2009
11. Aron and Poldrack., 2006	11. Sebastian et al., 2013	
12. Matsuda et al., 2004		
13. Jin et al., 2022		
Cluster 7: 131 voxels [Center: -34/-56/-26] Cerebellum Left VI	**Cluster 8: 103 voxels [Center: -50/4/2] Central Operculum Cortex**	**Cluster 9: 102 voxels [Center: -24/1/6] Putamen**
1. Damiani et al., 2024	1. Damiani et al., 2024	1. Sebastian et al., 2013
2. Latz et al., 2019	2. Cieslik et al., 2015	2. Aron and Poldrack., 2006
3. Georgiou-Karistianis et al., 2012	3. Sebastian et al., 2013	3. Aichert et al., 2011
4. Cai and Leung., 2009	4. Latz et al., 2019	4. Pastor et al., 2022
5. Eickhoff et al., 2011	5. Cai and Leung., 2009	5. Matsuda et al., 2004
6. Pastor et al., 2022	6. Maguire et al., 2003	6. Jarvstad et al., 2019
7. Kenner et al., 2010		7. Georgiou-Karistianis et al., 2012
8. Aichert et al., 2011		8. Eickhoff et al., 2011
9. Aron and Poldrack., 2006		9. Damiani et al., 2024
		10. Kawashima et al., 1996

Note: The publications are arranged according to the highest number of voxels contributed to a specific cluster.

Forced Two-Choice Response Selection with Respond and Not-Respond Options

23 experiments; 2,013 unique subjects (average of 87.5 per experiment)

Cluster 1: 668 voxels [Center: -4/4/52] **Pre-supplementary Motor Area (PreSMA)**	**Cluster 2: 516 voxels [Center: -46/-4/51]** **Precentral Gyrus**	**Cluster 3: 516 voxels [Center: 40/-82/-4]** **Lateral Occipital Cortex, inferior division**
1. Harding et al., 2016 2. King et al., 2015 3. Kaminski et al., 2019 4. Krug et al., 2008 5. Habel et al., 2007 6. Fukuda et al., 2019 7. Schneider et al., 2007 8. Takeuchi et al., 2018 9. Verhallen et al., 2021 10. Heinzel et al., 2016 11. Wu et al., 2017 12. Daamen et al., 2015 13. Baglio et al., 2011 14. Fedota et al., 2014 15. Schlagenhauf et al., 2008 16. Mostofsky et al., 2003 17. Li et al., 2014 18. Liddle et al., 2001	1. Harding et al., 2016 2. Fukuda et al., 2019 3. Kaminski et al., 2019 4. Heinzel et al., 2016 5. Wu et al., 2017 6. Schneider et al., 2007 7. Takeuchi et al., 2018 8. Habel et al., 2007 9. Li et al., 2014 10. King et al., 2015 11. Daamen et al., 2015 12. Krug et al., 2008 13. Mostofsky et al., 2003 14. Philip et al., 2016 15. Schlagenhauf et al., 2008 16. Baglio et al., 2011 17. Watanabe et al., 2002 18. Liddle et al., 2001	1. Kaminski et al., 2019 2. Harding et al., 2016 3. Daamen et al., 2015 4. Fukuda et al., 2019 5. Li et al., 2019 6. Heinzel et al., 2016 7. Habel et al., 2007 8. Wu et al., 2017 9. Schlagenhauf et al., 2008 10. Li et al., 2014 11. Verhallen et al., 2021 12. Fedota et al., 2014 13. Krug et al., 2008 14. Baglio et al., 2011 15. Takeuchi et al., 2018
Cluster 4: 265 voxels [Center: -42/-74/-6] **Lateral Occipital Cortex, inferior division**	**Cluster 5: 237 voxels [Center: 30/-54/-26]** **Cerebellum Right VI**	**Cluster 6: 200 voxels [Center: 60/-34/18]** **Planum Temporale**
1. Harding et al., 2016 2. Kaminski et al., 2019 3. Fukuda et al., 2019 4. Daamen et al., 2015 5. Li et al., 2019 6. Baglio et al., 2011 7. Wu et al., 2017 8. Heinzel et al., 2016 9. Schlagenhauf et al., 2008 10. Takeuchi et al., 2018 11. Verhallen et al., 2021	1. Harding et al., 2016 2. King et al., 2015 3. Takeuchi et al., 2018 4. Liddle et al., 2001 5. Wu et al., 2017 6. Habel et al., 2007 7. Mostofsky et al., 2003 8. Krug et al., 2008 9. Daamen et al., 2015 10. Li et al., 2014 11. Heinzel et al., 2016 12. Watanabe et al., 2002 13. Baglio et al., 2011	1. Wu et al., 2017 2. Kaminski et al., 2019 3. Fukuda et al., 2019 4. Schneider et al., 2007 5. Habel et al., 2007 6. Daamen et al., 2015 7. Baglio et al., 2011 8. Krug et al., 2008 9. Smits et al., 2009
Cluster 7: 197 voxels [Center: 34/20/6] **Insular Cortex**	**Cluster 8: 153 voxels [Center: -24/6/6]** **Putamen**	**Cluster 9: 134 voxels [Center: -26/-90/-4]** **Occipital Fusiform Gyrus, inferior division**
1. Habel et al., 2007 2. Harding et al., 2016 3. Daamen et al., 2015 4. Schneider et al., 2007 5. Heinzel et al., 2016 6. Krug et al., 2008 7. Kaminski et al., 2019 8. Fukuda et al., 2019 9. Smits et al., 2009	1. Wu et al., 2017 2. Harding et al., 2016 3. Pfefferbaum et al., 2001 4. Krug et al., 2008 5. Takeuchi et al., 2018 6. Fukuda et al., 2019 7. Daamen et al., 2015 8. Li et al., 2014 9. Liddle et al., 2001	1. Harding et al., 2016 2. Li et al., 2019 3. Fukuda et al., 2019 4. Habel et al., 2007 5. Heinzel et al., 2016 6. Li et al., 2014 7. Daamen et al., 2015 8. Fedota et al., 2014 9. Wu et al., 2017 10. Kaminski et al., 2019 11. Schlagenhauf et al., 2008

Cluster 10: 133 voxels [Center: -34/-56/-28] Cerebellum Left VI	Cluster 11: 116 voxels [Center: 2/-70/-15] Cerebellum Vermis VI	Cluster 12: 100 voxels [Center: 52/4/45] Precentral Gyrus
1. Wu et al., 2017 2. Heinzel et al., 2016 3. Habel et al., 2007 4. Krug et al., 2008 5. Takeuchi et al., 2018 6. Liddle et al., 2001 7. Mostofsky et al., 2003 8. Baglio et al., 2011 9. Harding et al., 2016	1. King et al., 2015 2. Schneider et al., 2007 3. Wu et al., 2017 4. Krug et al., 2008 5. Takeuchi et al., 2018 6. Daamen et al., 2015 7. Fukuda et al., 2019 8. Habel et al., 2007	1. Takeuchi et al., 2018 2. Daamen et al., 2015 3. Schneider et al., 2007 4. Wu et al., 2017 5. Kaminski et al., 2019 6. Fukuda et al., 2019 7. Harding et al., 2016 8. Verhallen et al., 2021

Note: The publications are arranged according to the highest number of voxels contributed to a specific cluster.