fMRI Investigation of Speed–Accuracy Strategy Switching

Antonino Vallesi,^{1,2*} Anthony R. McIntosh,^{1,3} Cristiano Crescentini,² and Donald T. Stuss^{1,3,4}

¹Rotman Research Institute at Baycrest, Toronto, Canada ²International School for Advanced Studies (SISSA-ISAS) – Cognitive Neuroscience Sector – Trieste, Italy ³Department of Psychology, University of Toronto, Toronto, On, Canada ⁴Department of Medicine, University of Toronto, Toronto, On, Canada

Abstract: Switching between rapid and accurate responses is an important aspect of decision-making. However, the brain mechanisms important to smoothly change the speed–accuracy strategy remain mostly unclear. This issue was addressed here by using functional magnetic resonance imaging (fMRI). On each trial, right-handed healthy participants had to stress speed or accuracy in performing a color discrimination task on a target stimulus according to the instructions given by an initial cue. Participants were capable of trading speed for accuracy and vice versa. Analyses of cue-related fMRI activations revealed a significant recruitment of left middle frontal gyrus and right cerebellum when switching from speed to accuracy. The left superior parietal lobule was activated in the same switching condition but only after the target onset. The anterior cingulate cortex was more recruited, also after target presentation, when speed had to be maintained from one trial to the next. These results are interpreted within a theoretical framework that attributes a role in criterion-setting to the left lateral prefrontal cortex, perceptual evidence accumulation to the superior parietal lobule, and action energization to the anterior cingulate cortex, extending previous findings to the domain of speed–accuracy tradeoff regulations. *Hum Brain Mapp* 33:1677–1688, 2012. © 2011 Wiley Periodicals, Inc.

Keywords: speed-accuracy trade off; prefrontal cortex; criterion setting; fMRI; decision making

INTRODUCTION

To dynamically trade speed for accuracy and vice versa according to external or internal contingencies is not only possible [Fitts, 1966; Woodworth, 1899] but also ecologi-

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cally advantageous [Chittka et al., 2009]. For instance, a safe-driving mode under no time–pressure might change into a faster one if a passenger in the car unexpectedly needs medical attention. Conversely, a fast-driving style is likely to become more cautious with a sudden storm. Although these processes do not occur very often in real-life, they are critical in many situations, and they can be studied in a controlled lab-setting, where strategic control can be effectively used to flexibly and continuously switch between rapid and accurate decision-making depending on payoffs [Swensson, 1972], deadlines [Pachella et al., 1968] and instructions [Hale, 1969].

To the best of our knowledge, the mechanisms underlying the switch between speed and accuracy strategies have not been considered by previous neuroimaging and psychological studies, although this factor seems critical for a successful interaction between the behavior and the

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^{*}Correspondence to: Antonino Vallesi, Scuola Internazionale Superiore di Studi Avanzati (SISSA-ISAS), via Bonomea 265, 34136 Trieste, Italy. E-mail: vallesi@sissa.it

external environment. Two previous functional magnetic resonance imaging (fMRI) studies [Ivanoff et al., 2008; van Veen et al., 2008] have shown an involvement of dorsolateral prefrontal cortex (DLPFC) in adjustments of baseline activity in decision-related cortical regions to balance between speed and accuracy. However, those studies have manipulated speed–accuracy instructions block-wise. A third recent study [Forstmann et al., 2008] used an eventrelated design but did not focus on the processes necessary to move from a strategy to another. Thus, the brain mechanisms important to dynamically switch the speed– accuracy strategy trial-by-trial remain unclear. This issue was addressed here by using fMRI during a color estimation task while randomly stressing either speed or accuracy at the beginning of each trial.

Multimodal imaging evidence shows that the left DLPFC is involved in setting up the initial task-criteria or producing a strategy in several domains, including episodic memory encoding [Kim et al., 2009; Kirchhoff, 2009; Rossi et al., 2001], task-switching [Brass and von Cramon, 2004], and cognitive conflict resolution [Banich et al., 2000; Floden et al., 2011; MacDonald et al., 2000]. It is therefore reasonable to expect that this region plays a critical role in triggering the task-relevant processes, especially when accurate decision-making has to follow a fast strategy (switch-to-accuracy trials). Given that the left PFC shows high sensitivity to practice [e.g., Shallice et al., 2008; Vallesi et al., 2009, 2011], we controlled for this factor by using a prescanning familiarization phase that stabilized performance and, inside the MRI scanner, we focused on switching between two already acquired strategies.

Aside from criterion-setting, a number of other processes are required in regulating the speed-accuracy trade off. Superior medial regions, including presupplementary motor area (pre-SMA) and anterior cingulate cortex, may play a critical role in maintaining response speed, given that lesions in this region consistently produce a response slowing in several tasks [Paus, 2001; Shallice et al., 2008; Stuss et al., 2005], while its activation is negatively correlated with Response Times (RT) [e.g., Mulert et al., 2003; Naito et al., 2000] and adjustments of the response threshold in the case of pre-SMA [Forstmann et al., 2008]. Thus, it is plausible that these regions are selectively activated under speed (vs. accuracy) instructions, and possibly more when response speed needs to be maintained across trials.

An influential theory of cognitive control posits that anterior cingulate monitors the occurrence of conflict in information processing while lateral prefrontal cortex implements the strategy to overcome this conflict [MacDonald et al., 2000; see Botvinick et al., 2004; Ridderinkhof et al., 2004, for reviews]. The fronto-medial wall, and in particular the anterior cingulate, has intensive reciprocal connections with the DLPFC [Bates and Goldman-Rakic, 1993; Petrides and Pandya, 1999]. Moreover, functional connections have also been described between the two structures [Derfuss et al., 2004; Koski and Paus, 2000; Paus et al., 2001]. These factors make it difficult to establish how cognitive control is realized in the brain, that is, which of these regions monitors conflicting situations when cognitive control is necessary, and which actually implements the control. The evidence is controversial: while several neuroimaging studies attribute a conflict monitoring function to ACC [e.g., Botvinick et al., 2004], some lesion studies suggest that the role of this region might be less critical with respect to that of lateral prefrontal regions, since conflict-induced behavioral adjustments are preserved after lesions within the ACC but diminish after lesions within the DLPFC [Gehring and Knight, 2000; Mansouri et al., 2007].

To further dissociate these two important functions in the context of speed–accuracy trade off regulations, an initial cue instructed the participants to stress either speed or accuracy (strategy production), while the actual target on which to perform the task (strategy implementation) appeared only after a variable interval. The duration of this variable interval varied according to a jittering procedure intended to optimize the separation of the hemodynamic response functions associated to the two critical events (cue and target), thus eluding orthogonality issues [Henson, 2006]. We reasoned that if a region is critical for the initial criterion-setting, it is expected to show enhanced cue-related activation. Conversely, target-related activation should be diagnostic of regions involved in actually implementing the speed–accuracy strategy.

METHOD

Participants

Twelve healthy volunteers (six females; mean age: 24 years, range: 19–37) took part in the study after signing an informed consent previously approved by the Ethics Research Board of Baycrest. All the participants had normal or corrected-to-normal vision. All were right-handed, as assessed with the Edinburgh Handedness Inventory [Old-field, 1971; average score: 89, range: 50–100). None reported any history of psychiatric or neurological disorders. Participants received 50 dollars in compensation for their time.

Experimental Material and Design

Visual stimuli were squares of 100 mm² presented centrally against a constantly gray background. Lighter and darker gray pixels randomly dispersed in the square frame (50% each) were used to form cue stimuli. Orange and green pixels were randomly dispersed in the square in various ratios (44/56, 47/53, 53/47, and 56/44) to form target stimuli [cf. Voss et al., 2004]. Cues were triplets of capital letters (SPD, for speed, or ACC for accuracy) appearing on the top of the cue stimulus at the beginning of the trial and disappearing with the target offset.

A first familiarization run without speed-accuracy instructions, and two practice runs with speed-accuracy



Figure I.

A schematical illustration of the experimental task performed during the fMRI session. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

instructions and visual feedback were previously performed in a mock scanner simulating MRI noise. Six experimental runs without feedback were subsequently performed inside the MRI scanner. A structural MRI was taken after three fMRI runs inside the scanner.

Each trial began with a cue stimulus lasting for 1,000 ms. The cue square was followed by a blank screen (with the cue letter string still present on the top of the screen), which lasted for a jittered random interval that was drawn from an exponential distribution generated using Chris Rorden's fMRI design software (http://www.sph.sc.edu/ comd/rorden/workshop/bic/fmridesign/index.html). This manipulation aimed at distinguishing the fMRI activations associated to the cue stimulus from those associated to the closely presented target stimuli. The mean of the exponential distribution of the jittered intervals was 3 s, with a minimum interval of 2 s and a maximum interval of 7.5 s. After this interval, the target stimulus was presented and stayed on the screen for 3 s. A blank screen with random jitter varying continuously from 4 to 6 s was then presented before the next trial began. In each run, the four green/orange proportions were presented pseudorandomly and equiprobably. In the runs with cue (all but the first familiarization run), the combination of two cue type (ACC vs. SPD) and two switch (cue switch vs. no-switch with respect to the previous trial) factors was also presented pseudorandomly and with the same probability.

The task was to judge which color (green or orange) was the predominant one in the target square by means of a forced-choice response with the index and middle fingers of the right hand (button 1 or 2). The association between prevailing color and response button was counterbalanced between-subjects. In a first baseline run inside the mock scanner, participants were asked to simply perform this task. During the next two practice runs with feedback, par-

ticipants were required to stress either speed or accuracy according to whether the triplet of letters appearing on the top of the cue at the beginning of the trial was SPD or ACC, respectively. Visual feedback was displayed for 2 s after each trial in which participants failed to obey the speed-accuracy rule. That is, if ACC was displayed as a cue, participants received feedback when they made a mistake in judging the target prevalent color (Wrong, be careful!). If SPD was displayed as a cue, participants received feedback in trials where their RT was larger than the mean RT plus 1/2 SD as calculated in the first baseline run (Try to be faster!). Finally, participants performed six experimental runs without feedback inside the scanner. A representation of the trial structure is presented in Figure 1. A blank screen was presented for 20 s at the beginning and for 30 s at the end of each run. Each run was composed of 40 experimental trials, and lasted about 8.5 min.

Image Acquisition and Data Preprocessing of fMRI Data

Images were acquired at the Baycrest Hospital on a 3 T Siemens Magnetom Trio whole-body scanner with a matrix 12-channel head coil. Head movements were minimized by appropriate cushioning. Functional volumes were obtained using a whole head T2*-weighted echo-planar image (EPI) sequence (repetition time, TR: 2 s, echo time, TE: 30 ms, flip angle: 70°, 28 oblique axial slices with interleaved acquisition, $3.1 \times 3.1 \times 5 \text{ mm}^3$ voxel resolution, field of view, FOV: 20 cm, acquisition matrix: 64 \times 64). Anatomical images were acquired using a MP-RAGE sequence (TR: 2 s, TE: 2.63 s, 160 oblique axial slices, with a 1 mm³ voxel size, FOV: 25.6 cm, acquisition matrix: 256 \times 256), after the first three functional runs. Visual stimuli were projected to a mirror mounted on the coil and optimally oriented for each participant. Manual responses were collected through a response pad.

The fMRI data preprocessing and statistical analyses were performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm/). For each participant, 1,572 fMRI volumes were acquired but the first five volumes of each run were discarded to allow for T1 equilibration. All the other volumes were then corrected for differences in the timing of slice acquisition, spatially realigned using a six-parameter rigid body head motion correction, coregistered to a standard MNI template (EPI.nii), spatially smoothed (8-mm Gaussian kernel), and high-pass filtered (128-s cutoff).

Behavioral Data Analysis

Accuracy and RT data were analyzed by means of a 2×2 repeated-measures ANOVA with cue type (accuracy vs. speed) and switch status (switch vs. no-switch) as the within-subject variables, separately for the prescanning practice phase with feedback (two runs collapsed) and for the scanning test phase (six runs collapsed).

We also submitted performance data from the fMRI phase to a diffusion model analysis [e.g., Ratcliff, 1978; Spaniol et al., 2006; Voss and Voss, 2007], an approach that decomposes the RT and accuracy data into underlying psychological processes, and correlated the obtained parameters with the activated brain regions to better understand how they regulate speed/accuracy strategies. The diffusion model assumes that two-choice RTs can be decomposed into nondecisional processes (perceptual analysis, motor execution) and a set of decisional processes whose duration is determined by systematic and random factors. The model parameter t_0 represents the nondecisional processes. The model parameter v (drift rate) indicates the strength of the systematic influence that drifts the decision process from a starting point (parameter z) to one of two response thresholds. As soon as a response threshold is reached, the decision process terminates, and a response is initiated. Finally, the distance between response thresholds is captured by the model parameter *a*. This parameter thus indicates how much information is required before either response is initiated (in our case: correct vs. incorrect color judgment). Large values of a produce on average more accurate but slower responses. Thus, this parameter is critical to determine which region is involved in changing response criteria from one strategy to the other.

The fast-dm method introduced by Voss et al. [2004] was employed to estimated the parameters of the diffusion model in a single modeling step, by using a Simplex downhill search to optimize the fit between the predicted and the empirical distributions [see Voss and Voss, 2007, for details]. We allowed *z*, *v*, and *a* to vary with each of the four conditions (two cue type × two switch), while the other parameters were assumed to be common to all conditions. Similar to RTs and accuracy data, the values of each of these parameters were assessed with separate 2 × 2 repeated-measures ANOVAs, with cue type and switch status as the within-subject factors.

fMRI Data Analysis

The fMRI time-series of each participant were best fitted at each voxel using the onsets of the critical conditions as obtained with a design given by the combination of the following factors: event type (cue and target), cue type (accuracy and speed), switch status (no-switch and switch), and difficulty level, which was nested within the target events only (difficult green/orange proportions: 47/53 and 53/47; easy proportions: 44/56 and 56/44). Since the latter factor did not show any significant effect, it was collapsed in the subsequent second-level analyses to increase power. The error trials and the first trial of each run (which did not have a switch status) were also modeled with a separate regressor but were not analyzed further. The six motion correction parameters were also included in the design matrix as covariates of no interest. An event-related approach was used and fMRI time-series were convolved with the SPM8 canonical hemodynamic response function at each voxel starting from cue onsets and target onsets of the critical conditions. Linear contrasts estimated the mean effect of the events of interest across the six fMRI runs.

Two separate group analyses were carried out for cues and targets using a general linear model with random effects. Significant brain activations that resulted from the contrasts of interest were isolated through paired t-tests. The study focuses on the brain mechanisms underlying the switching between speed and accuracy strategies. Therefore, besides from the main effects of cued strategy (speed vs. accuracy; accuracy vs. speed) and strategy switch (switch vs. no-switch; no-switch vs. switch), the following effects were analyzed. For the cue analysis, the interactions between cue type and switch status were extracted (first interaction: no-switch accuracy: -1, switchto-accuracy: 1, no-switch speed: 1, switch-to-speed: -1; second interaction: no-switch accuracy: 1, switch-to-accuracy: -1, no-switch speed: -1, switch-to-speed: 1). These interactions would capture any differential effect of switching from speed to accuracy when compared with switching from accuracy to speed on the pattern of brain activations. Moreover, the following simple main effects of interest were also extracted: switch vs. no-switch for accuracy and speed separately; no-switch vs. switch for accuracy and speed separately; and then the "switch-to-accuracy vs. all the rest" relevant contrast.

Similar to the cue analysis, all the main effects (speed vs. accuracy; accuracy vs. speed; switch vs. no-switch; noswitch vs. switch) and the two crossover interactions between previous cue type and switch status were also extracted for the target analysis. To better focus on effects of interest, the following contrasts were also computed: switch vs. no-switch for accuracy and speed separately; no-switch vs. switch for accuracy and speed separately; and then the "speed no-switch vs. all the rest," and "switch-to-accuracy vs. all the rest" relevant contrasts. Statistical threshold was set to P = 0.05 corrected for multiple comparisons at the cluster level (voxels within each cluster had an uncorrected *P*-level = 0.001), considering the whole brain as the volume of interest, unless otherwise specified.

RESULTS

Behavioral Results

Behavioral data are reported in Figure 2.

Practice Phase

RTs

A cue main effect [F(1,11) = 56.8, P < 0.001] indicated faster responses after a speed cue (843 ± 48 ms) than after an accuracy one (1,263 ± 82 ms). The switch main effect was not significant (P = 0.79). However, a cue by switch



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Behavioral data. Panels (**A**) and (**B**) show mean RTs (and standard error of the mean) in milliseconds, for the prescanning practice phase and for the fMRI test phase, respectively, according to cue type (x-axis) and switch status (bars). Panels (**C**) and (**D**)

interaction [F(1,11) = 14.5, P < 0.01] indicated that, for accuracy trials, responses were faster for switch (1,215 ± 88 ms) than no-switch (1,311 ± 79 ms) condition, while for speed trials, responses were faster for no-switch (801 ± 51 ms) than switch (885 ± 50 ms) trials, a result which suggests that the ability to get faster or slower according to initial cues benefits from repeating the same cue across trials, at least in the initial practice phase.

Accuracy

There was a main effect of switch only [F(1,11) = 5.4, P < 0.05], indicating that participants were more accurate in no-switch trials (91.9 \pm 2%) than in switch trials (89.4 \pm 1.9%). Participants tended to be more accurate after an

show the mean percentage of correct responses (and standard error of the mean), for the prescanning practice phase and for the fMRI test phase, respectively, according to cue type (x-axis) and switch status (bars).

accuracy cue (92.7 \pm 1.2%) than after a speed cue (88.1 \pm 2.8%) [Cue main effect: *F*(1,11) = 3.04, *P* = 0.1]. The cue by switch interaction was not significant (*P* = 0.58).

fMRI Phase

RTs

There was a cue main effect only [F(1,11) = 21.2, P < 0.001], due to participants being faster after a speed cue (906 ± 63 ms) than after an accuracy one (1,200 ± 68 ms). The switch main effect (P = 0.36) and the cue by switch interaction (P = 0.27) did not reach significance, probably due to practice effects and to the relatively slow pace of cue-target presentations, which may have allowed more

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		MNI coordinates		ates			
Anatomical localization	BA	x	у	z	Cluster <i>p</i> -corr.	Peak <i>z</i> -value	Voxels per cluster
Cue-related analysis							
Switch vs. no-switch							
Right posterior cerebellum		34	-46	-44	= 0.059 (unc = 0.005)	4.46	173
Interaction cue \times switch (switch	to ACC	and SPD	maintena	nce) vs. (4	ACC maintenance and swit	ch to SPD)	
Left middle frontal gyrus	9	-32	30	28	= 0.05	4.97	178
Left putamen		-26	4	10	< 0.001	4.23	387
Switch-to-accuracy vs. all the oth	er condi	tions					
Left middle frontal gyrus	9	-32	30	28	= 0.15 (unc. $= 0.01$)	5.01	126
Left caudate body		-22	-4	32	= 0.009	4.44	275
Switch vs. no-switch (accuracy)							
Left middle frontal gyrus	9	-32	30	28	< 0.05	5.55	192
Right posterior cerebellum	—	34	-44	-40	< 0.001	5.51	405
Target-related analysis							
Speed vs. accuracy							
Left supramarginal gyrus	40	-62	-52	36	= 0.028	3.67	198
Switch vs. no-switch							
Left sup. parietal lobule	7	-38	-70	54	< 0.0001	4.41	471
Interaction cue \times switch (switch	to ACC	and SPD	maintena	nce) vs. (4	ACC maintenance and swit	ch to SPD)	
Left posterior cerebellum	_	-26	-60	-42	= 0.002	4.97	336
Switch-to-accuracy vs. all the oth	er condi	tions					
Left sup. parietal lobule	7	-34	-76	48	< 0.0001	4.58	525
Switch vs. no-switch (accuracy)							
Left sup. parietal lobule	7	-34	-76	48	< 0.0001	5.37	1234
Left inferior frontal cortex	46	-46	36	10	= 0.009	3.97	258
Speed maintenance vs. the rest							
Left anterior cingulate c.	24	-2	24	14	= 0.016	4.75	225
No-switch vs. switch (speed)							
Left posterior cerebellum	_	-24	-64	-40	= 0.036	4.33	186
Speed vs. accuracy (no-switch)							
Left anterior cingulate c.	24	-2	24	14	= 0.009	4.97	256
Right supramarginal gyrus	40	56	-42	34	= 0.034	4.09	189
Left supramarginal gyrus	40	-56	-44	30	= 0.017	3.93	224

TABLE I. Significant cluster activations in SPM analyses

BA, Brodmann area.

time to adopt a speed–accuracy strategy without extra behavioral costs. An extra ANOVA including also the factor run (six levels) was performed to check for residual learning effects inside the scanner. This analysis showed only a cue main effect [F(1,11) = 21.62, P < 0.001] and a run main effect [F(5,55) = 3.35, P = 0.01]. The latter was due to a RT decrease from run 3 to run 6 only (post-hoc Tukey HSD P = 0.026). Importantly, there was no interaction between run and either cue type (P = 0.184) or switch status (P = 0.165), and no three-way interaction (P = 0.29), thus excluding specific learning effects during the fMRI session.

Accuracy

There was a cue main effect [F(1,11) = 5, P < 0.05], indicating that participants were more accurate after being instructed to be accurate (89 \pm 1.4%) than to be fast (84 \pm 3.1%). The switch main effect (P = 0.18) and the cue by

switch interaction (P = 0.88) did not reach significance. An ANOVA including the factor run (six levels) again produced a cue main effect only [F(1,11) = 5, P < 0.05], with all the effects involving the run factor being far from significance (for all, P > 0.31), thus excluding learning effects.

Diffusion model

The model fit was quite good for all participants, as assessed by the Kolmogorov–Smirnov test (for all, *P* range 0.29–0.89). The only significant effect concerned the distance between response thresholds, parameter *a*. This parameter was higher for accuracy cues than for speed cues [2.04 vs. 1.48, respectively; cue type main effect: F(1,11) = 26.5, P < 0.001]. This result indicates that response criteria became stricter when an accuracy strategy was adopted as compared with a speed strategy. Moreover, no-switch trials tended to have higher drift rates (parameter *v*) than switch ones [main effect of switch, P = 0.076], suggesting

that, due to systematic influences, the decision process tended to drift towards a response threshold more quickly during no-switch trials than during switch ones.

fMRI data

Table I reports significant clusters produced in the contrasts of interest for both cue-related and target-related activity. The contrasts that are not reported are those which did not generate significant clusters.

Cue effects

The crossover interaction contrasting switch-to-accuracy and speed maintenance against accuracy maintenance and switch-to-speed showed two significant clusters in left DLPFC (BA 9) and left putamen. This interaction suggests that these regions might have a differential role in switching depending on which strategy is going to be activated. Indeed, the left DLPFC was also significantly activated in the more detailed contrast between switch-to-accuracy and accuracy maintenance (Fig. 3A). This contrast also activated the right posterior cerebellum. The left DLPFC additionally showed more activation, together with the left caudate body, in switch-to-accuracy condition vs. the other three conditions, although in the latter case multiple comparisons correction showed a significant activation at the peak level only (corrected P = 0.016; uncorrected P at the cluster level = 0.01). The key condition that consistently shows left DLPFC activation, therefore, is the switch-to-accuracy condition. Activation (beta values) of left DLPFC (6-mm radius sphere around the peak) in this condition showed a positive correlation with accuracy (r = 0.59, P < 0.590.05, see Fig. 3A), indicating that the participants who activated this region more when an initial cue instructed them to switch from speed to accuracy were then more accurate in estimating the prevalent color of the target. The activity of the peak voxel in left DLPFC was also positively correlated with the distance between response thresholds (parameter *a*), selectively in switch-to-accuracy trials (r = 0.61, P < 0.05), indicating that higher DLPFC activation was associated with stricter response criteria in this condition (for the other three conditions, P range 0.14–0.26).

Target effects

The crossover interaction contrasting switch-to-accuracy and speed maintenance against accuracy maintenance and switch-to-speed produced a significant activation cluster in left posterior cerebellum. The more detailed contrast between switch-to-accuracy and accuracy maintenance showed significant clusters in the left superior parietal lobule (Fig. 3B) and left inferior frontal gyrus. Contrasting switch-to-accuracy against all the three other conditions also produced activation of the left superior parietal lobule, which in this condition showed a negative correlation with RTs (r = -0.6, P < 0.05, see Fig. 3B), but no significant correlation with any of the diffusion model parameters. Taken together, these results strongly suggest that the left superior parietal lobule plays a critical role in the switching-to-accuracy condition. However, this role seems to be mainly related to accuracy strategy implementation, since this region is activated after the target presentation and not during the cue phase. Moreover, the fact that activation in this region correlates with speed fits well with its evidence accumulation function.

The left supra-marginal gyrus was activated in the contrast between speed and accuracy. The more detailed contrast between speed and accuracy on no-switch trials produced activation in the bilateral supramarginal gyrus and in the anterior cingulate cortex. Importantly, the latter activation also emerged when contrasting speed maintenance trials vs. all the rest (Fig. 3C), consistent with models attributing a motor energization function to the anterior cingulate [see Paus, 2001; Stuss et al., 2005].

DISCUSSION

The present fMRI study investigated the neural mechanisms underlying speed–accuracy trade off regulations during a color estimation task. After a practice phase, participants were able to trade speed for accuracy and vice versa, according to an initial instructional cue which was randomly varied trial-by-trial. Moreover, a diffusion model analysis showed that the process that was significantly different when an accurate strategy was applied, as compared with a fast one, was a decisional process which sets a higher distance between response criteria (parameter *a* of the diffusion model). On the other hand, the evidence drift rate, the decisional starting point and nondecisional processes were not modulated by the speed–accuracy strategy manipulation.

Cue-related fMRI analysis showed a key role of the left DLPFC specifically when switching from speed to accuracy, as seen in the contrast between switch-to-accuracy and accuracy maintenance and in the contrast between switch-to-accuracy and the other three conditions. A cue by switch interaction demonstrated that this region is selectively activated in switching to accuracy and not in switching to speed, probably because this region is specifically involved in adopting a stricter criterion. This activation indeed positively correlated with subsequent accuracy in the color estimation task and with distance between response criteria (parameter a), suggesting a role of left DLPFC in increasing the sensitivity in task performance by adopting stricter decision-criteria. Switching to accuracy, when contrasted with remaining in an accuracy mode, also activated the right posterior cerebellum. This region has been shown to be critical in inhibiting the contralateral M1 [Galea et al., 2009; Koch et al., 2008; Oliveri et al., 2005; but see Fierro et al., 2007], as it would be required when an accuracy strategy has to be adopted and a speed strategy has to be abandoned.

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Figure 3.

Main brain clusters activated in task-relevant contrasts. Panels $(\mathbf{A}-\mathbf{C})$ indicate activations, beta values, and brain-behavior correlations for left middle frontal gyrus (in cue-related period), left superior parietal lobule and anterior cingulate (in target-related period), respectively. See Table I for a more detailed report of the activated clusters. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Switching to accuracy (accuracy-after-speed trials) and maintaining speed (speed-after-speed trials) also activated the left putamen in the initial cue phase, as evidenced by the contrast regarding the crossover cue \times speed interaction. Such activation under different task conditions suggests multiple functions of this region of the striatum. The activation of the putamen during switch-to-accuracy trials is consistent with a role of this region in inhibiting inappropriate motor programs [Mink, 1996], while its activation in speed maintenance trials fits with its role in preparing task-relevant movements [Alexander et al., 1986, 1990]. Alternatively, Forstmann et al. [2008; see also van Veen et al., 2008] propose that the striatum plays a role in maintaining speed by reducing the inhibitory control of the basal ganglia over the motor system, thus allowing a quicker but probably premature response. This study suggests that this is true especially when the speed pressure lasts for multiple trials.

The target-related analysis showed a dissociation between superior and inferior portions of the posterior parietal cortex. The left superior parietal cortex (BA 7) was mostly activated when switching from speed to accuracy but only after target presentation (contrasts: switch-to-accuracy vs. accuracy maintenance, and switch-to-accuracy vs. the other three conditions). Activation in this region after target presentation negatively correlated with RTs in the switch-to-accuracy condition, indicating that the participants who responded faster activated this region more. Although a correlation with speed may seem at odds with a condition in which response slowing is required, this is consistent with a role of this region in accumulating evidence for a sensorimotor decision [Gold and Shadlen, 2002; Hanks et al., 2006; Huk and Shadlen, 2005; Shadlen and Newsome, 2001]. Roitman and Shadlen [2002], for instance, showed that in monkeys a decision is made once the accumulation of evidence in lateral intraparietal sulcus for one response or another reaches a threshold value, threshold value that is probably established earlier in the left prefrontal cortex. It is important to observe that the activation of this region during switch-to-accuracy cannot be accounted for as the sole consequence of longer RTs and decisional processes under accuracy vs. speed instructions (and a proportionally larger BOLD response), because RTs in this condition were as long as in the accuracy maintenance condition (after the practice phase, when they were even shorter), and yet this region was not activated in the latter condition (see Fig. 3B, middle panel).

On the other hand, a more inferior cluster in the supramarginal gyrus (BA 40) was more activated when the target was presented under speed than under accuracy instructions. The activation in the supramarginal gyrus was left-lateralized although it became bilateral in speed maintenance trials. The left supramarginal gyrus is related to motor attention, a function which seems to be independent of the moving hand [see PET evidence by Rushworth et al., 2001a,b; also see Snyder et al., 2006].

This dissociation between superior parietal lobule (switch-to-accuracy) and inferior parietal lobe (speed maintenance) also fits with a recent model of parietal cortex fractionation, which was originally proposed in the memory domain [Cabeza et al., 2008]. On that model, the superior parietal cortex is involved in top-down attentional allocation to task-relevant information, consistent with its activation when greater attention to the perceptual evidence is required to switch from speed to accuracy. On the other hand, inferior parietal cortex is more involved in automatic attention to the available evidence, consistent with its activation under time pressure (speed maintenance trials).

Target-related activity was also found in left PFC, although more inferiorly than cue-related activity, especially during switch-to-accuracy trials (vs. accuracy maintenance), consistent with the proposal that this region is also implicated in accumulating [Noppeney et al., 2010] and integrating [Heekeren et al., 2006] the sensory input supporting perceptual decisions [see Gold and Shadlen, 2007]. A left hemispheric network including DLPFC, medial prefrontal, and parietal cortices has been proposed to be specialized for response selection [Rubia et al., 2001] and perceptual decision-making [Kayser et al., 2010]. We found that the left DLPFC (cue-related activity) temporally precedes left superior parietal cortex (target-related activity) when switching from speed to accuracy, a result that strongly suggests that these two regions have temporally dissociable functions: stimulus-independent criterion-setting and perceptual evidence accumulation, respectively. Importantly, primary sensory and motor areas were not differentially involved in speed-accuracy modulations, further suggesting that speed-accuracy adjustments in decision making take place in higher-level fronto-parietal networks [see Ivanoff et al., 2008].

Noteworthy, the anterior cingulate cortex was mostly activated in the target-period, when it was necessary to maintain a fast response from one trial to the next (contrasts: speed maintenance vs. accuracy maintenance; speed maintenance vs. the other three conditions), consistently with his role in response energization [Naito et al., 2000; Paus, 2001; Stuss et al., 2002, 2005]. This finding shows that, in the present task, the anterior cingulate cortex is more involved in the maintenance of demanding motor responses rather than in the monitoring and detection of difficult events such as a cue requiring high accuracy [cf. Botvinick et al., 2004; Frank et al., 2007; Ridderinkhof et al., 2004], consistent with the fact that it is connected with the motor, striatal and limbic system in a more direct way than DLPFC [Haber, 2003; Picard and Strick, 1996; Takada et al., 2001; see Paus, 2001, for a review]. A preliminary analysis (not reported here) contrasting difficult (47/ 53 pixel color ratios) vs. easy (44/56 pixel color ratios) target conditions did not show any reliable brain activation, therefore confirming that anterior cingulate activity found here is not related to difficulty per se.

An alternative hypothesis would be that increased timepressure in decision-making might increase the error likelihood and, in turn, the need for performance monitoring [Botvinick et al., 2004] or error detection [Kiehl et al., 2000; Menon et al., 2001]. However, the current fMRI analysis was restricted to correct trials and no correlation between accuracy and ACC activation was found in this study, suggesting that this link is unclear. The fronto-medial wall, and in particular the anterior cingulate, has intensive reciprocal connections with the DLPFC [e.g., Bates and Goldman-Rakic, 1993]. Given the rich reciprocal connections between the two regions [e.g., Derfuss et al., 2004; Paus et al., 2001], it is usually difficult to detect the specific contributions of each of them to cognitive control. This study demonstrates the usefulness of separating different phases of a task in order to disentangle the role of different prefrontal subregions in neuroimaging studies.

The present results are fully consistent with the fractionation model of prefrontal cortex proposed by Stuss and colleagues [e.g., Shallice et al., 2008; Stuss et al., 2002, 2005], according to which left prefrontal regions are involved in criterion-setting and strategy production, while superior medial prefrontal regions are more dedicated to motor energization. This model is itself consistent with that proposed by Alexander et al. [1986, 1990], since the separate regions demonstrated in the frontal fractionation studies and here map onto the separate frontal cortical nodes belonging to different cortico-basal gangliathalamic loops [Stuss, 2007].

Recent fMRI studies [Forstmann et al., 2008; see Bogacz et al., 2010, for a review] found that speed instructions were associated with activations in the striatum and pre-SMA, a region located more dorsally and posteriorly than the anterior cingulate cluster activated here, which the authors interpreted as important for the release of motor areas from inhibition and adjustments of response threshold. Although pre-SMA showed higher activation for speed than for accuracy instructions, this was far from significance. One possible account of this discrepancy is that participants in our task were well-trained (three blocks of trials) before entering the scanner, and that pre-SMA plays a more critical role in speeding up responses during a learning phase. Another possibility is the fact that the analyses reported here focused on correct trials only, presumably when there is still some control over fast but careless responding. Future studies with a higher number of error trials should further investigate whether, under time pressure, errors are more associated with pre-SMA and striatum activation than correct responses.

Finally, behavioral switch "costs" (i.e., being slower and less accurate when switching from a strategy to another) were present during the practice phase but disappeared during the fMRI phase, suggesting that participants fully acquired the appropriate mechanisms to smoothly switch from one strategy to another. While we intentionally introduced a practice phase to exclude learning-related accounts [cf. Vallesi et al., 2009], it is possible that similar or related brain mechanisms are also required to acquire, and not only to apply, the ability to flexibly switch between speed and accuracy strategies.

A possible limitation of the study is that a color estimation task only was used to regulate speed/accuracy strategy. Further research adopting more than one task should elucidate whether the brain regions activated in the different phases of speed–accuracy trade off regulation are involved in a task-independent manner [see Fleck et al., 2006, for a similar approach].

CONCLUSIONS

This study showed that not only adopting speed and accuracy strategies per se [Förster et al., 2003; Ivanoff et al., 2008; Trimmer et al., 2008; van Veen et al., 2008], but also dynamically switching between them requires different mechanisms. The left DLPFC is associated to dynamic regulation of speed–accuracy trade off. It sets strict response criteria, preparing the task-relevant processes necessary to allow accurate decisions following faster and more liberal responding. The superior parietal lobule then implements this strategy. The anterior cingulate contribution seems relevant during repeated fast responding. Future neuropsychological or TMS research is required to probe the causality of these associations. Consistent with the present neuroimaging results, a dysfunction in the left lateral prefrontal territory is expected to impair the implementation of an accuracy strategy when switching from a speed strategy, while impairment in superior medial prefrontal regions would hinder speed maintenance.

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REFERENCES

- Alexander GE, Crutcher MD, DeLong MR (1990): Basal gangliathalamocortical circuits: Parallel substrates for motor, oculomotor, "prefrontal" and "limbic" functions. Prog Brain Res 85:119–146.
- Alexander GE, DeLong MR, Strick PL (1986): Parallel organization of functionally segregated circuits linking basal ganglia and cortex. Annu Rev Neurosci 9:357–381.
- Banich MT, Milham MP, Atchley RA, Cohen NJ, Webb A, Wszalek T, Kramer AF, Liang Z, Barad V, Gullett D, Shah C, Brown C (2000): Prefrontal regions play a predominant role in imposing an attentional 'set': Evidence from fMRI. Brain Res Cogn Brain Res 10:1–9.
- Bates JF, Goldman-Rakic PS (1993): Prefrontal connections of medial motor areas in the rhesus monkey. J Comp Neurol 336:211–228.
- Bogacz R, Wagenmakers EJ, Forstmann BU, Nieuwenhuis S (2010): The neural basis of the speed-accuracy tradeoff. Trends Neurosci 33:10–16.
- Botvinick MM, Cohen JD, Carter CS (2004): Conflict monitoring and anterior cingulate cortex: An update. Trends Cogn Sci 8:539–546.
- Brass M, von Cramon DY (2004): Selection for cognitive control: A functional magnetic resonance imaging study on the selection of task-relevant information. J Neurosci 24:8847–8852.
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M (2008): The parietal cortex and episodic memory: An attentional account. Nat Rev Neurosci 9:613–625.
- Chittka L, Skorupski P, Raine NE (2009): Speed-accuracy tradeoffs in animal decision making. Trends Ecol Evol 24:400–407.
- Derfuss J, Brass M, von Cramon DY (2004): Cognitive control in the posterior frontolateral cortex: Evidence from common activations in task coordination, interference control, and working memory. Neuroimage 23:604–612.
- Fierro B, Giglia G, Palermo A, Pecoraro C, Scalia S, Brighina F (2007): Modulatory effects of 1 Hz rTMS over the cerebellum on motor cortex excitability. Exp Brain Res 176:440–447.
- Fitts PM (1966): Cognitive aspects of information processing. III. Set for speed versus accuracy. J Exp Psychol 71:849–857.
- Floden D, Vallesi A, Stuss DT (2011): Task context and frontal lobe activation in the stroop task. J Cogn Neurosci 23:867–879.

- Forstmann BU, Dutilh G, Brown S, Neumann J, von Cramon DY, Ridderinkhof KR, Wagenmakers EJ (2008): Striatum and pre-SMA facilitate decision-making under time pressure. Proc Natl Acad Sci USA 105:17538–17542.
- Förster J, Higgins ET, Bianco AT (2003): Speed/accuracy decisions in task performance: Built-in trade-off or separate strategic concerns? Organization Behav Hum Decision Process 90:148– 164.
- Fleck MS, Daselaar SM, Dobbins IG, Cabeza R (2006): Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. Cereb Cortex 16:1623–1630.
- Frank MJ, Scheres A, Sherman SJ (2007): Understanding decisionmaking deficits in neurological conditions: Insights from models of natural action selection. Philos Trans R Soc Lond B Biol Sci 362:1641–1654.
- Galea JM, Jayaram G, Ajagbe L, Celnik P (2009): Modulation of cerebellar excitability by polarity-specific noninvasive direct current stimulation. J Neurosci 29:9115–9122.
- Gehring WJ, Knight RT (2000): Prefrontal-cingulate interactions in action monitoring. Nat Neurosci 3:516–520.
- Gold JI, Shadlen MN (2002): Banburismus and the brain: decoding the relationship between sensory stimuli, decisions, and reward. Neuron 36:299–308.
- Gold JI, Shadlen MN (2007): The neural basis of decision making. Annu Rev Neurosci 30:535–574.
- Haber SN (2003): The primate basal ganglia: Parallel and integrative networks. J Chem Neuroanat 26:317–330.
- Hale DJ (1969): Speed-error tradeoff in a three-choice serial reaction task. J Exp Psychol 81:428–435.
- Hanks TD, Ditterich J, Shadlen MN (2006): Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. Nat Neurosci 9:682–689.
- Heekeren HR, Marrett S, Ruff DA, Bandettini PA, Ungerleider LG (2006): Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. Proc Natl Acad Sci USA 103:10023–10028.
- Henson RN (2006). Efficient experimental design for fMRI. In: Friston K, Ashburner J, Kiebel S, Nichols T, Penny W, editors. Statistical Parametric Mapping: The Analysis of Functional Brain Images. London: Elsevier. pp193–210.
- Huk AC, Shadlen MN (2005): Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. J Neurosci 25:10420–10436.
- Ivanoff J, Branning P, Marois R (2008): fMRI evidence for a dual process account of the speed-accuracy tradeoff in decisionmaking. PLoS One 3:e2635.
- Kayser AS, Buchsbaum BR, Erickson DT, D'Esposito M (2010): The functional anatomy of a perceptual decision in the human brain. J Neurophysiol 103:1179–1194.
- Kiehl KA, Liddle PF, Hopfinger JB (2000): Error processing and the rostral anterior cingulate: An event-related fMRI study. Psychophysiology 37:216–223.
- Kim AS, Vallesi A, Picton TW, Tulving E (2009): Cognitive association formation in episodic memory: Evidence from eventrelated potentials. Neuropsychologia 47:3162–3173.
- Kirchhoff BA (2009): Individual difference in episodic memory: The role of self-initiated encoding strategies. Neuroscientist 15:166–179.
- Koch G, Mori F, Marconi B, Codeca C, Pecchioli C, Salerno S, Torriero S, Lo GE, Mir P, Oliveri M, Caltagirone C (2008): Changes in intracortical circuits of the human motor cortex fol-

lowing theta burst stimulation of the lateral cerebellum. Clin Neurophysiol 119:2559–2569.

- Koski L, Paus T (2000): Functional connectivity of the anterior cingulate cortex within the human frontal lobe: A brain-mapping meta-analysis. Exp Brain Res 133:55–65.
- MacDonald AW, Cohen JD, Stenger VA, Carter CS (2000): Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288:1835–1838.
- Mansouri FA, Buckley MJ, Tanaka K (2007): Mnemonic function of the dorsolateral prefrontal cortex in conflict-induced behavioral adjustment. Science 318:987–990.
- Menon V, Adleman NE, White CD, Glover GH, Reiss AL (2001): Error-related brain activation during a Go/NoGo response inhibition task. Hum Brain Mapp 12:131–143.
- Mink JW (1996): The basal ganglia: Focused selection and inhibition of competing motor programs. Prog Neurobiol 50:381–425.
- Mulert C, Gallinat J, Dorn H, Herrmann WM, Winterer G (2003): The relationship between reaction time, error rate and anterior cingulate cortex activity. Int J Psychophysiol 47:175–183.
- Naito E, Kinomura S, Geyer S, Kawashima R, Roland PE, Zilles K (2000): Fast reaction to different sensory modalities activates common fields in the motor areas, but the anterior cingulate cortex is involved in the speed of reaction. J Neurophysiol 83:1701–1709.
- Noppeney U, Ostwald D, Werner S (2010): Perceptual decisions formed by accumulation of audiovisual evidence in prefrontal cortex. J Neurosci 30:7434–7446.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97–113.
- Oliveri M, Koch G, Torriero S, Caltagirone C (2005): Increased facilitation of the primary motor cortex following 1 Hz repetitive transcranial magnetic stimulation of the contralateral cerebellum in normal humans. Neurosci Lett 376:188–193.
- Pachella RG, Fischer DF, Karsh R (1968): Absolute judgments in speeded tasks: Quantification of the trade-off between speed and accuracy. Psychonom Sci 12:225–226.
- Paus T (2001): Primate anterior cingulate cortex: Where motor control, drive and cognition interface. Nat Rev Neurosci 2:417–424.
- Paus T, Castro-Alamancos MA, Petrides M (2001): Cortico-cortical connectivity of the human mid-dorsolateral frontal cortex and its modulation by repetitive transcranial magnetic stimulation. Eur J Neurosci 14:1405–1411.
- Petrides M, Pandya DN (1999): Dorsolateral prefrontal cortex: Comparative cytoarchitectonic analysis in the human and the macaque brain and corticocortical connection patterns. Eur J Neurosci 11:1011–1036.
- Picard N, Strick PL (1996): Motor areas of the medial wall: A review of their location and functional activation. Cereb Cortex 6:342–353.
- Ratcliff R (1978): A theory of memory retrieval. Psychol Rev 85:59–108.
- Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S (2004): The role of the medial frontal cortex in cognitive control. Science 306:443–447.
- Roitman JD, Shadlen MN (2002): Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J Neurosci 22:9475–9489.
- Rossi S, Cappa SF, Babiloni C, Pasqualetti P, Miniussi C, Carducci F, Babiloni F, Rossini PM (2001): Prefrontal [correction of prefontal] cortex in long-term memory: An "interference" approach using magnetic stimulation. Nat Neurosci 4:948–952.

- Rubia K, Russell T, Overmeyer S, Brammer MJ, Bullmore ET, Sharma T, Simmons A, Williams SC, Giampietro V, Andrew CM, Taylor E (2001): Mapping motor inhibition: Conjunctive brain activations across different versions of go/no-go and stop tasks. Neuroimage 13:250–261.
- Rushworth MF, Krams M, Passingham RE (2001a): The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. J Cogn Neurosci 13:698–710.
- Rushworth MF, Paus T, Sipila PK (2001b): Attention systems and the organization of the human parietal cortex. J Neurosci 21:5262–5271.
- Shadlen MN, Newsome WT (2001): Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. J Neurophysiol 86:1916–1936.
- Shallice T, Stuss DT, Picton TW, Alexander MP, Gillingham S (2008): Mapping task switching in frontal cortex through neuropsychological group studies. Front Neurosci 2:79–85.
- Snyder LH, Dickinson AR, Calton JL (2006): Preparatory delay activity in the monkey parietal reach region predicts reach reaction times. J Neurosci 26:10091–10099.
- Spaniol J, Madden DJ, Voss A (2006): A diffusion model analysis of adult age differences in episodic and semantic long-term memory retrieval. J Exp Psychol: Learn Mem Cogn 32:101–117.
- Stuss DT (2007): New approaches to prefrontal lobe testing. In: Miller B, Cummings J, editors. The Human Frontal Lobes: Functions and Disorders, 2nd ed. New York: Guilford Press. pp 292–305.
- Stuss DT, Alexander MP, Shallice T, Picton TW, Binns MA, Macdonald R, Borowiec A, Katz DI (2005): Multiple frontal systems controlling response speed. Neuropsychologia 43:396–417.

- Stuss DT, Binns MA, Murphy KJ, Alexander MP (2002): Dissociations within the anterior attentional system: Effects of task complexity and irrelevant information on reaction time speed and accuracy. Neuropsychology 16:500–513.
- Swensson RG (1972): The elusive trade-off: Speed vs. accuracy in visual discrimination tasks. Percept Psychophys 12:16–32.
- Takada M, Tokuno H, Hamada I, Inase M, Ito Y, Imanishi M, Hasegawa N, Akazawa T, Hatanaka N, Nambu A (2001): Organization of inputs from cingulate motor areas to basal ganglia in macaque monkey. Eur J Neurosci 14:1633–1650.
- Trimmer PC, Houston AI, Marshall JA, Bogacz R, Paul ES, Mendl MT, McNamara JM (2008): Mammalian choices: Combining fast-but-inaccurate and slow-but-accurate decision-making systems. Proc Biol Sci 275:2353–2361.
- Vallesi A, McIntosh AR, Alexander MP, Stuss DT (2009): FMRI evidence of a functional network setting the criteria for withholding a response. Neuroimage 45:537–548.
- Vallesi A, McIntosh AR, Stuss DT (2011). Over-recruitment in the aging brain as a function of task demands: Evidence for a compensatory view. J Cogn Neurosci 23:801–815.
- van Veen V, Krug MK, Carter CS (2008): The neural and computational basis of controlled speed-accuracy tradeoff during task performance. J Cogn Neurosci 20:1952–1965.
- Voss A, Rothermund K, Voss J (2004): Interpreting the parameters of the diffusion model: An empirical validation. Mem Cogn 32:1206–1220.
- Voss A, Voss J (2007): Fast-dm: A free program for efficient diffusion model analysis. Behav Res Method 39:767–775.
- Woodworth RS (1899): The Accuracy of voluntary movement. Psychol Rev 3:1–119.