Tracking Perceptual and Memory Decisions by Decoding Brain Activity

van Vugt, Marieke; Brandt, Armin; Schulze-Bonhage, Andreas

Published in:
BIAS 2017 preproceedings

Publication date:
2017

Tracking Perceptual and Memory Decisions by Decoding Brain Activity

Marieke van Vugt[1], Armin Brandt[2], Andreas Schulze-Bonhage[2]

[1] Institute of Artificial Intelligence & Cognitive Engineering, University of Groningen, The Netherlands m.k.van.vugt@rug.nl
[2] Epilepsy Center, University Medical Center Freiburg, Germany

Abstract. Decision making is thought to involve a process of evidence accumulation, modelled as a drifting diffusion process. This modeling framework suggests that all single-stage decisions involve a similar evidence accumulation process. In this paper we use decoding by machine learning classifiers on intracranially recorded EEG (iEEG) to examine whether different kinds of decisions (perceptual vs. memory) exhibit dynamics consistent with such drift diffusion models. We observed that decisions are indeed decodable from brain activity for both perceptual and memory decisions, and that the time courses for these types of decisions appear to be quite similar. Moreover, the high spatial resolution of iEEG revealed that perceptual and memory decisions rely on slightly different brain areas. While the accuracy of decision decoding can stil be improved, these initial studies demonstrate the power of decoding analyses for testing computational models of cognition.

1 Introduction

Decision making is a basic cognitive process that comes to play in many different tasks. Most of the research on decision making focuses on simple tasks such as detecting the direction of randomly moving dots. The theories developed on the basis of those experiments presume that all decisions between two alternatives (at least those consisting of a single stage process) behave with similar dynamics. Specifically, according to drift diffusion models (DDMs; Ratcliff, 1978), decisions follow a drifting diffusion process, where the random walk is driven by the decision information. The DDM starts the process of evidence accumulation at the moment the stimulus comes on the screen, and then slowly drifts towards one of the decision thresholds which each correspond to a particular decision option. As soon as the decision threshold is reached, the response corresponding to the relevant decision option is given. The model has been found to produce excellent fits to performance in a variety of tasks, as well as the detailed shape of the associated response time distributions. The parameters of this model each can be interpreted as specific cognitive processes such as attention allocation in the drift rate parameter and speed-accuracy trade-off in the location of the decision threshold (Ratcliff, 2016). In addition to the drift rate and the decision threshold, the third main parameter of the model is the non-decision time, which

reflects non-decision-related processes such as preparing a motor response and fixed delays in the perceptual system. By varying the values of these parameters, subtle differences in shapes of the response time distributions can be reproduced.

While DDMs were developed exclusively based on behavioral data, more recently it has also been suggested that the brain may implement such diffusion processes. For example, in seminal work, Shadlen and colleagues observed monotonously increasing firing rates of neurons in the lateral intraparietal area while monkeys were deciding about the direction of randomly moving dots (Shadlen and Newsome, 1996, Roitman & Shadlen, 2002). This neural signature was modulated by the strength of the decision evidence (the proportion of dots moving coherently) and the traces seemed to all move up to the same final firing rate around the time of the response. Subsequent studies on monkeys in similar tasks instead placed evidence accumulation in the frontal eye fields (Ferrera et al., 2009, Hanes & Schall, 1996, Purcell et al., 2010), superior colliculus (Ding & Gold, 2012) and caudate (Ding & Gold, 2010). Some of the differences between studies could be traced back to the response modality (e.g., accumulation-like activity is more likely in frontal eye field when monkeys use saccades to indicate their response than when they use reaching).

In humans, accumulation processes have been studied as well, although in that case the challenge is the trade-off between poor temporal resolution of functional magnetic resonance imaging (fMRI) and the poor spatial resolution of electroencephalograph (EEG). FMRI studies have suggested evidence accumulation may take place in the dorsolateral prefrontal cortex (Heekeren et al., 2006), inferior frontal gyrus (Ho et al., 2009, Krueger et al., 2017, Ploran et al., 2007) but as demonstrated in a meta-analysis, in fact almost the whole brain (Mulder et al., 2014). Using EEG, we found neural correlates of evidence accumulation in parietal 4–9Hz theta oscillations when people were making decisions about randomly moving dots (van Vugt et al., 2012). MEG (magnetoencephalography) studies have implicated different brain regions in the accumulation process, such as 14–24Hz beta oscillations over motor cortex; Donner et al., 2009). In addition to these brain oscillations, it has been suggested that two event-related potentials–the centroparieto potential (CPP; O'Connor et al., 2012), and the lateralized readiness potential (van Vugt et al., 2014)–reflect evidence accumulation. While the CPP may arise from parietal cortex, the lateralized readiness potential may come from premotor areas of the brain. However, none of this localization is very specific since it is derived from scalp-recorded EEG, which has poor localization.

An alternative approach to localizing the decision process in the brain has been to use classifiers, which are increasingly popular in neuroscience. The first studies using these methods focused on finding specific moments in time at which decisions can be best classified, rather than tracking the complete decision process over time. For example, Ratcliff and colleagues (2009) found that a logistic regression-based classifier in the period around 400 ms post-stimulus exhibited behavior consistent with evidence accumulation during a face-car discrimination task–the output of this classifier covaried with between-trial differences in the

drift rate. Philliastides and colleagues (2014) followed up on this in a similar face-house discrimination task and showed that a Fisher discriminant analysis could also track the decision process over time and this process appeared to be predominantly localized to parietal regions.

While these results are promising, they do not give very detailed localization of the decision process and restrict themselves to the cortex due to the inherent constraints of EEG data. Moreover, as is clear from the above discussion, different studies have claimed that evidence accumulation occurs in many different brain areas, dependent on the study. One potential reason for contradictory results may be that decisions on the basis of different kinds of evidence may be implemented by different brain regions. For this reason, it is worthwhile to examine whether evidence accumulation looks similar for different kinds of decisions, such as perceptual decisions and decisions about remembered information.

To enhance spatial localization we decode decision information from intracranially-recorded brain oscillations (rather than the scalp EEG used in most previous studies). Intracranial EEG is data with a high degree of spatial and temporal precision that can be obtained from epileptic patients who are implanted with electrodes for clinical purposes (Jacobs & Kahana, 2010). To determine what brain areas are involved in decision making, and where the decision information is available over time, we ran a regularized logistic regression classifier in short (50-ms) time bins, and assessed how classification accuracy develops for memory and perceptual decisions. We focused on classifying 4–9Hz theta oscillations, since we previously demonstrated that those are most informative for decision making (van Vugt et al., 2012). We then looked at the classifier weights to determine what Brodmann areas carry most of the decision information, and whether those differed between perceptual and memory decisions.

2 Methods

2.1 Participants

Participants were recruited from the patients undergoing long-term invasive monitoring for pharmacologically intractable epilepsy at Freiburg University hospital (Germany). Sixteen individuals were recruited and participated in our behavioral experiments.

2.2 Task

To be able to compare perceptual and memory decisions, we created a task with perceptual and memory conditions that used the same set of stimuli. We created synthetic face stimuli by means of the Basel Face model (Paysan et al., 2009), which allowed us to manipulate the stimulus similarity (and hence task difficulty) very precisely. In the perceptual condition (Fig. 1(a)), participants saw two faces facing outward and had to determine whether this face belonged to the same person (i.e., was simply a rotated version of the same face). In the

memory condition (Fig. 1(b)), participants were first shown two faces during a 2000–2075ms (jittered) study period, followed by a 1000–1150ms (jittered) blank delay period, after which a probe face was shown. Participants were then asked to indicate by a button press whether this probe face was identical to one of the two faces presented in the study. The jitter in the task was used to ensure that no spurious oscillatory phase-locking could occur.

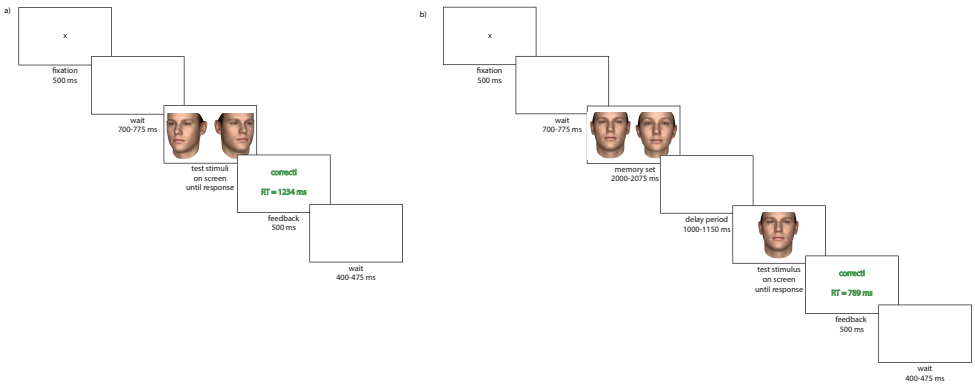

Fig. 1. Example trials of the perceptual (a) and memory (b) condition.

2.3 Recordings

Data were recorded with a 2000Hz sampling rate on the clinical EEG recording system (Compumedics). We then segmented the data into trials of 4000 ms duration, starting 200 ms prior to the onset of the probe stimulus. We checked for the occurrence of epileptiform activity and one of the participants' data had to be discarded due to epileptic spikes in a majority of the trials. Trials whose response time exceeded the trial segment duration (3800 ms) were discarded, and the classifier analysis was done only on correct trials. Similarly, trials with a kurtosis larger than 15 (indicative of epileptic spikes) were removed. The total dataset involves 1178 electrodes.

2.4 Data analysis

Data were analyzed by means of in-house matlab code that was based on toolboxes developed by Jelmer Borst and Per Sederberg. First, we ensured that the two classes to be separated (match/non-match decisions) had an equal number of trials by randomly removing trials from the larger class. We then performed a wavelet transform to obtain EEG time courses in the 4–9Hz theta band, which previously has been shown to be important for decision making (van Vugt et al., 2012). Next, we z-transformed all trials to ensure the data had an average of zero and a standard deviation of one. We then vincentized the data–that is, we turned each trial into an equal number of bins between the stimulus and

the response (with the exception of the first 300 ms, which contains roughly the same peaks irrespective of the response time, so this period was not stretched or compressed and simply divided into 6 bins of 50 ms duration). The number of bins was chosen such that on average, bin duration would be approximately 50 ms.

For each time bin, we trained a regularized logistic regression model to distinguish between the match and non-match responses. Essentially, this model tries to find a matrix $\mathbf{W}$ that maps between the n x p matrix of examples $\mathbf{X}$ (p is the number of features, n is the number of trials) and the vector of labels (match or non-match) Y: $\mathbf{W} = (\mathbf{X}^T\mathbf{X} + \lambda\mathbf{I}_p)^{-1}\mathbf{X}^T Y$. In this equation, I_p is the p x p identity matrix and λ is the regularization matrix. The regularization allows the algorithm to deal with many correlated predictors. For each classifier the regularization parameter lambda was determined by means of a search between 0 and 10,000 (Borst et al., 2013). The lambda that minimized the root-mean-square prediction error across all labels was chosen. We then assessed the classifier's performance using 10-fold cross-validation.

3 Results

3.1 Accuracy across subjects

We first examined how well decisions could be decoded from intracranial EEG data per participant. Fig. 2 illustrates the maximum accuracy across the decision interval (between the moment the probe stimulus came on the screen and the response). As can be seen, there are large differences between individuals in classification accuracy, which ranges from close to chance (55%) to 76%. Most accuracies significantly exceed chance according to a binomial proportion test (see stars in Fig. 2; $p < 0.016$, reflecting a 5% False Discovery Rate).

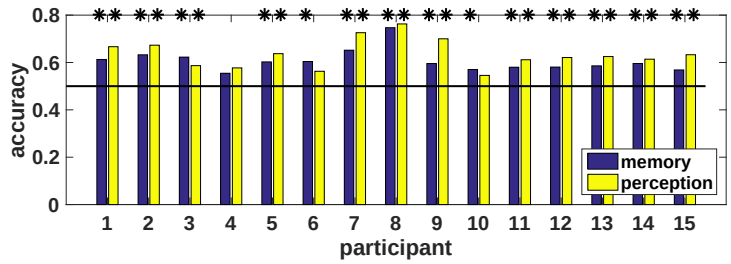

Fig. 2. Maximum decision decoding accuracy for each participant, separately for perceptual and memory trials. Stars indicate classification accuracies that are larger than chance.

Having established that decision classification is possible to some extent, we can now examine our main question: what is the time course of these classifications, and does it differ between perceptual and memory decisions? Fig. 3 demonstrates that while for some participants there is no classification possible, and

Table 1. DDM parameters (mean and standard error of the mean). Perceptual and memory trials were split between low and high-similarity conditions (difficult and easy, respectively). Decision threshold was kept fixed between all conditions. Non-decision time was fixed between the similarity conditions. This model came out as best from a BIC comparison of various model configurations.

condition	drift	decision threshold	non-decision time (s)
perception low similarity	-0.41 (0.13)	0.27 (0.025)	0.92 (0.15)
perception high similarity	0.24 (0.066)	0.27 (0.025)	0.92 (0.15)
memory low similarity	-0.11 (0.014)	0.27 (0.025)	0.50 (0.047)
memory high similarity	0.11 (0.016)	0.27 (0.025)	0.50 (0.047)

the signal hovers around chance level, for others there is meaningful classification, and consistent with the DDM, classification accuracy increases slowly over time (the slope of the classification accuracy is larger than zero for both memory decisions ($t(14)$=2.55, $p = 0.012$) and for perceptual decisions ($t(14)$=3.04, $p = 0.0044$)). Unexpectedly, classification accuracy appears to continue to increase even after the response has been made. One possible interpretation of such a pattern is provided by recent modeling studies that suggest that after the decision has been made, the accumulation process continues with the objective of estimating decision confidence (Pleskac & Busemeyer, 2010).

Comparing the two conditions, classifier accuracy appears to get higher for perception than for memory trials (M_{memory}=0.61; $M_{perception}$=0.64 ; $t(14)$=2.82, $p = 0.014$). In short, while perceptual and memory decisions involve quite different tasks and response times, the decodable decision information forms quite a similar trajectory for both, consistent with the DDM predictions. The only difference is that the classifiers start to increase at different points in time, presumably because the response time in the perception condition is significantly longer than in the memory condition. This difference in response time is presumably caused by the fact that in the perception condition, participants need to first mentally rotate the images before they can make their decision. DDM fits are consistent with this idea (see parameters in Tab. 1): there is a significant effect of task on the non-decision time parameter ($F(1, 60)$=14.1, $p = 0.0004$, similar to previous studies of mental rotation decisions). Another interesting finding is that classification accuracy appears to continue increasing even after the decision has been made. This is consistent with some findings from experiments with monkeys suggesting that after the decision has been made, participants continue to accumulate information to make estimates of their confidence in the decision.

3.2 How do different brain areas contribute to classification?

Next, we asked what brain areas are involved in classification, and how these regions differ between perceptual and memory decisions. Specifically, for every Brodmann area, we reported the proportion of electrodes in that area that were significantly involved in evidence accumulation (i.e., having z-scores larger than 2). Fig. 4 shows the electrodes that were, across participants most involved in

classification, separately for perception and memory decisions. It is clear that most of these electrodes are in lateral parietal and temporal areas. Part of the reason for that is of course that the locations that are relevant for clinical purposes tend to be temporal areas, which are often the sources of epileptic seizures. Table 2 demonstrates that the Brodmann areas that have the largest proportion of electrodes carrying decision information are parietal areas (Brodmann area 7) and perceptual-motor areas (Brodmann areas 1-2-3-5).

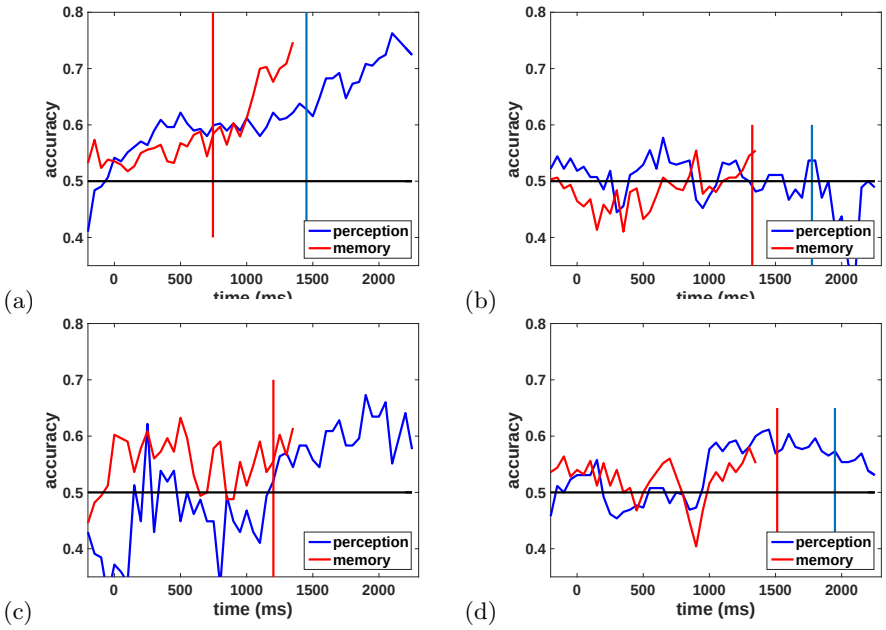

Fig. 3. Time courses of classification accuracy in the 4–9Hz theta band for a participant with good classification (a) and for a participant with poor classification (b). For comparison, two other participants are also shown ((c) and (d)). Vertical lines indicate the average time of the response for the relevant condition (blue for perception, red for memory).

Discussion

We examined the time course of the availability of decision information during a perceptual and a memory decision task. As the DDM predicted, overall the decoded decision evidence shows similar dynamics for perceptual and memory decisions. The difference between the two lies in the time at which they move upwards, which is later for the perception condition than for the memory condition. This is not surprising given that for the perception task the response time is significantly longer than in the memory task. The second question we asked was whether accumulation in the perception and memory conditions relies

on different brain regions. Because we have no full brain coverage we can only make tentative claims, but the data so far suggest that there are differences between those two types of decisions (see also Fig. 4). While memory decisions rely predominantly on Brodmann area 7 (parietal cortex) and sensorimotor cortex, perceptual decisions rely more on Brodmann area 13 (anterior insula) and 30 (visual area).

While we did obtain classification accuracies above chance, classification is far from stellar. Potentially other classifiers such as lasso or artificial neural nets could do better than these. On the other hand, such classifiers run a higher risk of overfitting the data. Another potential approach could be to make use of the known similarity structure of the face stimuli. Previous studies have shown that such decoded similarity structures can help to track memory representations in the brain (Zhang et al., 2015). In addition, we focused here on the theta band, because that frequency was suggested by prior studies. Nevertheless, it could easily be the case that for these data, better decision information could be decoded from other frequencies. Finally, there are large differences between individuals. We examined whether individual differences in task performance (accuracy and response time) could account for these differences in classification accuracy. We found that the data were too unreliable to make any connection between task performance and classifier accuracies (all Bayes Factors between 0.4 and 2.2).

Table 2. Proportion of significant electrodes by Brodmann area for classification of target-lure/match-nonmatch decisions on the basis of 4–9Hz theta activity. The Brodmann areas are ordered by proportion of significant electrodes. Only Brodmann areas with more than 15 electrodes are included. Brodmann areas for which the proportion of significant electrodes is zero: 9, 22, 28,40, 47 and hippocampus.

Brodmann area	memory	perception	$N_{electrodes}$	$N_{participants}$
Brodmann area 7	0.17	0.06	18	1
Brodmann area 13	0.03	0.09	34	10
Brodmann area 20	0.01	0.07	179	13
Brodmann area 36	0.02	0.07	46	9
Brodmann area 37	0.01	0.04	98	12
Brodmann area 41/42	0.03	0.03	33	8
Amygdala	0.00	0.03	31	9
Brodmann area 21	0.01	0.03	246	13
Brodmann area 19	0.02	0.00	57	9
Brodmann area 38	0.02	0.00	101	10

Another weaker part of this study is that it did not make a direct connection to DDM parameters. If the dynamics of the decoded decision process were to covary with model parameter estimates (van Vugt et al., 2012), this would bolster our confidence that we are in fact observing neural correlates of a drift diffusion process. One approach that we can use in the future to examine this is to use the classifier readout to separate the trials into low-evidence and high-evidence,

and then to fit the DDM separately to these classes of trials. Previous studies using such an approach have demonstrated that such within-participant model verification can be used to identify neural correlates of drift diffusion processes (Ratcliff et al., 2009; Ratcliff et al., 2016b).

In short, we have demonstrated how decoding decision information from brain data can help us to better understand the dynamics of decision making. This builds on a larger body of work that uses classifiers to track covert cognitive processes over time. As classifiers become more powerful and can deal with more noisy data, these are very useful tools to help us uncover how the brain "does" cognition. Moreover, we will gain a better and better time-resolved picture of cognitive processes, which can subsequently inform computational models of these processes.

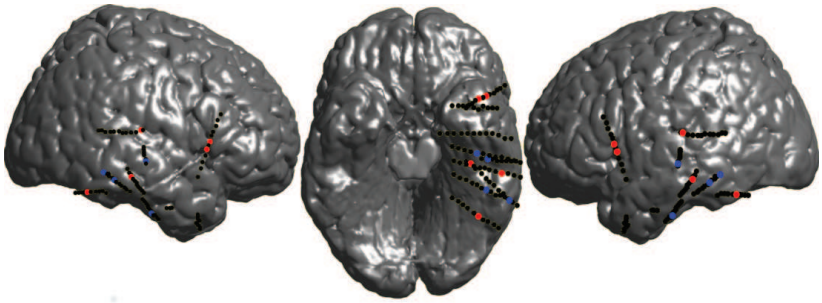

Fig. 4. Electrodes that contribute significantly (z>2) to decision classification. Black dots indicate electrodes that are not showing significant decision-related activity. Red: perceptual decisions. Blue: memory decisions. The electrode locations for two participants were missing, so those are not included in this figure and in Table 1. In addition, Brodmann areas having no electrodes in our dataset are also excluded from the table.

References

Ratcliff, R.: A theory of memory retrieval. Psychological Review **85** (1978) 59–108

Ratcliff, R., Smith, P.L., Brown, S.D., McKoon, G.: Diffusion decision model: current issues and history. Trends in Cognitive Sciences (2016)

Shadlen, M.N., Newsome, W.T.: Motion perception: seeing and deciding. Proc Natl Acad Sci U S A **93** (1996) 628–633

Roitman, J.D., Shadlen, M.N.: Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. J Neurosci **22**(21) (2002) 9475–9489

Ferrera, V.P., Yanike, M., Cassanello, C.: Frontal eye field neurons signal changes in decision criteria. Nature Neuroscience **12** (2009) 1458–1462

Hanes, D.P., Schall, J.D.: Neural control of voluntary movement initiation. Science **274** (1996) 427–430

Purcell, B.A., Heitz, R.P., Cohen, J.Y., Schall, J.D., Logan, G.D., Palmeri, T.P.: Neurally constrained modeling of perceptual decision making. Psychological Review **117**(4) (2010) 1113–

1143

Ding, L., Gold, J.I.: Neural correlates of perceptual decision making before, during, and after decision commitment in monkey frontal eye field. Cerebral Cortex **22** (2012) 1052–1067

Ding, L., Gold, J.I.: Caudate encodes multiple computations for perceptual decisions. J Neurosci **30** (2010) 15747–15759

Heekeren, H.R., Marrett, S., Ruff, D.A., Bandettini, P.A., Ungerleider, L.G.: Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. Proc. Nat. Acad. Sci., USA **103**(26) (2006) 10023–10028

Ho, T., Brown, S., Serences, J.T.: Domain general mechanisms of perceptual decision making in human cortex. J Neurosci **29**(27) (2009) 8675–8687

Krueger, P.M., van Vugt, M.K., Simen, P., Nystrom, L., Holmes, P., Cohen, J.D.: Evidence accumulation detected in BOLD signal using slow perceptual decision making. J Neurosci Meth **281** (2017) 21–32

Ploran, E.J., Nelson, S.M., Velanova, K., Donaldson, D.I., Petersen, S.E., Wheeler, M.E.: Evidence accumulation and the moment of recognition: dissociating perceptual recognition processes using fMRI. J Neurosci **27**(44) (2007) 11912–11924

Mulder, M.J., van Maanen, L., Forstmann, B.U.: Perceptual decision neurosciences - a model-based review. Neuroscience **277** (2014) 872–884

van Vugt, M.K., Simen, P., Nystrom, L., Holmes, P., Cohen, J.D.: EEG oscillations reveal neural correlates of evidence accumulation. Frontiers in Human Neuroscience **6** (2012) 106

Donner, T., Siegel, M., Fries, P., Engel, A.K.: Buildup of choice-predictive activity in human motor cortex during perceptual decision making. Current Biology **19** (2009) 1581–1585

O'Connell, R.G., Dockree, P.M., Kelly, S.P.: A supramodal accumulation-to-bound signal that determines perceptual decisions in humans. Nature Neuroscience **15**(12) (2012) 1729–1735

van Vugt, M.K., Simen, P., Nystrom, L., Holmes, P., Cohen, J.D.: Lateralized readiness potentials reveal properties of a neural mechanism for implementing a decision threshold. PLoS ONE **9**(3) (2014) e90943

Ratcliff, R., Philiastides, M., Sajda, P.: Quality of evidence for perceptual decision making is indexed by trial-to-trial variability of the EEG. Proc. Nat. Acad. Sci., USA **106**(16) (2009) 6539

Philiastides, M.G., Heekeren, H.R., Sajda, P.: Human scalp potentials reflect a mixture of decision- related signals during perceptual choices. J Neurosci **34**(50) (2014) 16877–16889

Jacobs, J., Kahana, M.J.: Direct brain recordings fuel advances in cognitive electrophysiology. Trends in Cognitive Sciences **14**(4) (2010) 162–171

IEEE: A 3D Face Model for Pose and Illumination Invariant Face Recognition, Genova, Italy, IEEE (2009)

Borst, J., Schneider, D.W., Walsh, M.M., Anderson, J.R.: Stages of processing in associative recognition: Evidence from behavior, EEG, and classification. J Cogn Neurosci **25**(12) (2013) 2151–2166

Pleskac, T., Busemeyer, J.R.: Two-stage dynamic signal detection: A theory of choice, decision time, and confidence. Psychological Review **117**(3) (2010) 864–901

Zhang, H., Fell, J., Staresina, B., Weber, B., Elger, C.E., Axmacher, N.: Gamma power reductions accompany stimulus-specific representations of dynamic events. Current Biology **25** (2015) 635–640

Ratcliff, R., Sederberg, P.B., Smith, T., Childers, R.: A single trial analysis of EEG in recognition memory: Tracking the neural correlates of memory strength. Neuropsychologia **93** (2016) 128–141

Provost, A., Heathcote, A.: Titrating decision processes in the mental rotation task. Psychological Review **122**(4) (2015) 735–754