Accumulation of Evidence in Perceptual Decisions

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Acknowledgments

Abstract

Recent research has accumulated insights into the neural processes underlying perceptual decision making by using mathematical models and neurophysiological experiments with monkeys. The studies performed on monkeys suggest that a decision is made by accumulating evidence in favor of the decision alternatives, until a decision threshold is reached. This process is closely linked to the planning of the motor response to a given choice, and the spike rate in the neurons performing this calculation show sustained activity until a response can be made. In order to investigate if an area in the human brain shows the same activations as accumulation neurons in the monkey brain, functional magnetic resonance imaging (fMRI) was used to record blood oxygenation level dependent (BOLD) responses while participants performed a forced two-choice perceptual decision making task with face and house stimuli containing a varying degree of visual noise. A 2 by 2 factorial design was used to investigate if there are brain regions that show both (a) greater activation for harder compared to easier trials in a reaction time task and (b) greater activation for easier compared to harder trials in a delayed response task. No such area was found, suggesting that humans rely on a different decision making mechanism than monkeys, where the accumulation of evidence is dissociated from the maintenance of the decision. The left intraparietal sulcus (IPS) and the dorsomedial prefrontal cortex (DMPFC) were identified as potential accumulator regions, showing more activity for hard than easy decisions across response conditions. A region in the left superior frontal gyrus was identified as a candidate for maintaining the decision until a response cue appears.

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Introduction

Perceptual decision making is the process of combining sensory evidence to form a decision. Such decisions guide our behavior directly, for instance when deciding on which side of a pedestrian it would be best to maneuver your bicycle in order to avoid a crash. Sequential sampling models (SSM) are mathematical models of the cognitive processes underlying such decisions. One of these models, Ratcliff's Diffusion Decision Model (DDM) (Ratcliff, 1978; Ratcliff & McKoon, 2008; Smith & Ratcliff, 2004) describes how decisions are made in two-alternative forced choice tasks. For an explanation of this model, consider viewing a visually noisy image, with the goal to decide whether this image contains a face or a house. The DDM assumes that when making decisions like this, the difference in evidence between the two alternatives is sampled continuously, until one of two decision boundaries is reached, and a decision to respond either face or house is made. As can be seen in Figure 1, in the DDM, such a decision process is represented by a sample path with a starting point z. The difference in evidence is continuously gathered until a boundary (a or o) is reached for one of the two alternatives. The accumulation rate describes how much evidence is gathered per sample. The process is noisy (within-trial variability), thus sometimes resulting in errors. According to the model, the accumulation rate is primarily influenced by the quality of evidence. Therefore, in easier tasks, the accumulation rate will be higher than in more difficult tasks. The decision boundary will be reached earlier with a high accumulation rate, resulting in a higher rate of accurate responses and shorter response times for easier tasks, due to noise having less effect on the outcome.

The DDM also assumes that the distance between the two boundaries will primarily be affected by time pressure. If a participant performing a perceptual task is told to focus on being as fast as possible, it will affect the distance between decision boundaries, which will be closer together than if the focus is to be as accurate as possible. This will result in faster response times but more errors for the speed condition, because noise will then have more influence on the outcome. When told to focus on accuracy, the response times will be slower, but the accuracy will be higher, because noise will not affect the decision as much. The DDM has been shown to provide excellent fits to behavioral data (Ratcliff & Smith, 2004; Smith & Ratcliff, 2004), accounting for the changes in accuracy and response time distributions following the aforementioned manipulations.
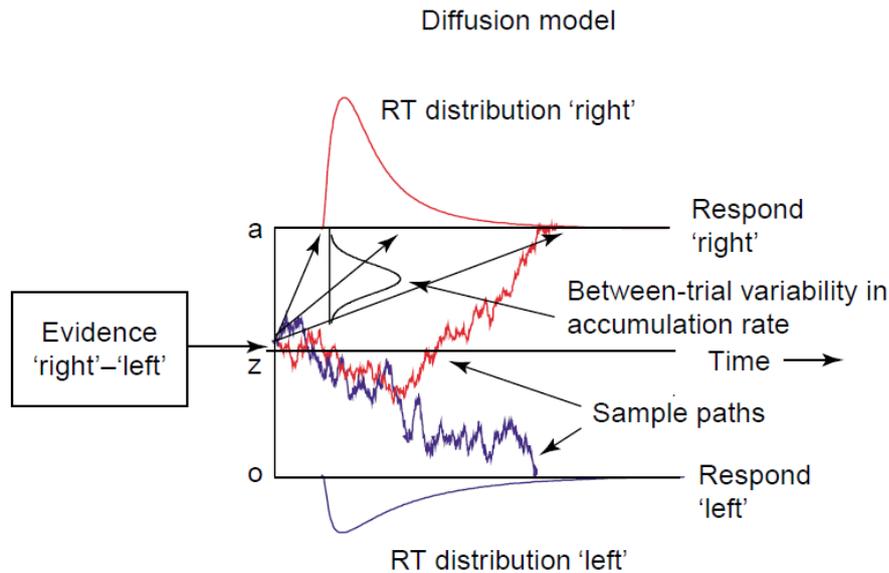
Diffusion model

RT distribution 'right'

a

Evidence
'right'–'left'

z

o

Respond
'right'

Between-trial variability in
accumulation rate

Time →

Sample paths

Respond
'left'

RT distribution 'left'

Figure 1. An overview of the main features of the DDM. Accumulation of evidence starts at a starting point (z). Evidence is gathered until a decision boundary is reached (a or o) and a response is made. Figure taken from Smith & Ratcliff (2004).

Recent advances in imaging techniques have made it possible to test if the DMM can also be used to describe the underlying neural mechanisms of decision making. To be able to do this, predictions about neural activity need to be derived from the DDM. Several such proposals have been made (e.g. Basten, Biele, Heekeren & Fiebach, 2010; Hare, Schultz, Camerer, O'Doherty & Rangel, 2011, Kayser, Buchsbaum, Erickson & D'Esposito, 2010; Purcell et al., 2010; Ratcliff, Cherian & Segraves, 2003). Shared by most of them is the assumption that for perceptual decisions, in a given task, lower level sensory regions should code evidence in favor of the alternatives, which will accumulated in a separate region, until a decision boundary is reached and a response is made.

Neurophysiological evidence for decision making mechanisms

Sensory evidence. Newsome and colleagues (Newsome, Britten & Movshon, 1989; Britten, Shadlen, Newsome & Movshon, 1992) were among the first to find properties of neurons translating perceptual stimuli into sensory evidence. These researchers used single cell recording on macaque monkeys trained to do a random dot motion task. In this task, a series of dots move randomly across a screen, except for a subset of dots that move coherently towards one of two opposing directions. The objective of the task is to decide in which direction the coherent dots are heading. In many of the experiments, the monkeys are trained to make a response with a saccade to one of two peripheral targets, placed on either side of the stimuli. Britten and colleagues (1992) reported neurons which were responsive to the

directions of the coherently moving dots in the middle temporal (MT) area. The spike rate of neurons within the MT area correlated positively with the degree of coherently moving dots in the direction to which they were responsive to. These neurons also showed the opposite pattern for the other direction; firing less the more dots moved coherently in the opposite direction. These activations have been reported in studies using different stimuli as well. For instance, in a vibrotactile frequency task (VTF) (Salinas, Hernandez, Zainos & Romo, 2000) the spike rate of a region within the primary somatosensory cortex (V1) could be used to predict the monkey's decisions. These results indicate that the type of stimuli depicts which sensory areas are involved.

Accumulation of evidence. In a study where monkeys performed an RDM task (Shadlen & Newsome, 2001), neurons within the lateral intraparietal area (LIP) were reported to accumulate evidence from neurons coding sensory evidence (within the MT). The LIP area, a part of the intraparietal sulcus in the parietal cortex, is involved in oculomotor planning (Colby & Goldberg, 1999), and could therefore be thought to be involved in decisions where saccades are used to obtain responses. Using a response cue design, with a delay period between stimulus presentation and response, neurons within the response field of one of the choice targets had a firing rate that correlated positively with the degree of motion in that direction. The neurons kept firing until a response could be given, and the firing rate declined immediately after giving a response. Later research, using the same paradigm with a reaction time (RT) condition (Roitman & Shadlen, 2002), also identified neurons accumulating evidence, but now a response was made as soon as a threshold to decide was reached. The responses were significantly faster for the easier decisions, due to the response threshold being reached earlier. Based on these results, and taking into account the DDM, it has been proposed that for RDM tasks with saccade-responses, sensory evidence is coded in neurons within the visual area MT while LIP neurons integrate the evidence until it reaches a threshold to form a decision[1].

Decision making mechanism. Studies using microstimulation have provided evidence that the visual area MT plays a causal role in coding sensory evidence in the RDM task. When

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[1] In light of these findings, the neurophysiological data favor a race model over the DDM. In race models (Usher & McClelland, 2001), it is assumed that evidence in favor of each alternative is accumulated in separate areas, and that the first to reach a decisions boundary wins the race. However, because the accumulator areas can be thought to be mutually inhibitory (Bogacz, 2007) the predictions of neural activity would be the same for both the DDM and race model. Therefore, the findings are explained here in terms of the DDM, which provides the best fit to behavioral data, while assuming that the neural implementation is more like a race model.

stimulating the motion selective MT neurons, monkeys showed a bias toward responding in favor of the preferred direction of the stimulated neurons (Salzman, Britten & Newsome, 1990; Salzman, Murasugi, Britten & Newsome, 1992). The same procedure has also been performed on LIP-neurons (Hanks, Ditterich & Shadlen, 2006). Comparing the effects the stimulations had on bias and response time shows that when stimulating MT-neurons responses are much more biased towards the preferred direction of the neurons than when stimulating the LIP-neurons (Gold & Shadlen, 2007). This is in line with the assumptions that MT-neurons code sensory evidence while the LIP-neurons accumulate the evidence, because biasing of the evidence is thought to have a constant additive effect towards one of the alternatives, while biasing of the accumulation-process in one direction would only change the starting point z towards that direction.

In addition to the LIP-neurons, neurons within the frontal eye fields (FEF) and the dorsolateral prefrontal cortex (DLPFC) have also been found to take part in accumulating evidence in visual perceptual tasks (Gold & Shadlen, 2000; Kim & Shadlen, 1999). These areas are also involved in selection and preparation of oculomotor action. The mechanism reported here of visual perceptual decision making extends to studies using tactile stimuli, involving areas including the second somatosensory cortex (Romo, Hernandez, Zainos, Lemus & Brody, 2002) and ventral premotor cortex (Romo, Hernández & Zainos, 2004). The findings from single-unit recording in monkeys in general support the hypothesis that evidence is gathered in lower-level sensory regions, and then accumulated in regions involved in motor planning. These activations support the basic assumptions of sequential sampling models. The activations seen in the accumulator neurons also suggest that both the decision and maintenance of the decision until the response cue occurs, is performed within the same neurons, as reported in the study using a delayed response paradigm, where neurons in the LIP region reached a threshold sooner for easier decisions, and kept firing until a response could be given (Shadlen & Newsome, 2001).

Neuroimaging evidence for decision making mechanisms

Using the knowledge gained from the studies using neurophysiological techniques with monkeys, and the predictions of the DDM, recent studies have investigated whether the human brain implements similar mechanisms the monkey brain. Due to the invasive nature of single-cell recordings, most studies performed with human participants have taken advantage of functional magnetic resonance imaging (fMRI). fMRI measures the blood oxygenation

level dependent (BOLD) response, which is correlated with neuronal activity (Logothetis, Pauls, Augath, Trinath, Oeltermann, 2001; Logothetis & Pfeuffer, 2004)

Sensory evidence. Results from neuroimaging studies suggest a similar process for coding of sensory evidence in the human brain as that reported for monkeys, in which the sensory regions involved in coding evidence depend on the type of stimuli. One of the first studies using fMRI in a simple perceptual decision task with human participants found areas in the temporal pole which seemed to code sensory evidence (Heekeren, Marrett, Bandettini & Ungerleider, 2004). These researchers used a face-house paradigm, with pictures that were either easy or difficult to identify, manipulated by adding varying degrees of noise to the images. Displaying properties of sensory evidence coding, both the fusiform face area (FFA) and parahippocampal place area (PPA), showed stronger activation when viewing faces and houses, respectively. Further, the FFA was activated more strongly for face images with less noise than those with more. The same effect was found for houses in the PPA. In a random dot motion task, coding of sensory evidence was reported to be performed in the visual area MT+ (Kayser et al., 2010), homologues to the MT-region reported in the neurophysiological studies. The MT+ area had a higher BOLD response for low-coherence trials, the opposite of what was found using single-unit recording. The reason for this disparity is the low spatial resolution of fMRI, resulting in measuring the entire MT+, thus including all preferred directions. With a low level of coherence it was assumed that several neurons fired weakly, while with a high coherence, only the neurons for the preferred direction were activated, with the remaining neurons at rest. The same activation was also found in another study using the RDM task (Ho, Brown & Serences, 2009), but in this study it was predicted that the MT+ area would fire more for harder trials due to representing the sensory evidence for a longer period of time when the decision is difficult. A study using value-based tasks, where the goal was to choose stimuli that maximized gains and minimized losses, reported that the ventral striatum and amygdala (Basten et al., 2010) coded gains and losses, respectively. In accordance with the results from the neurophysiological studies, the regions involved in coding of sensory evidence depend on the type of stimuli used.

Accumulation of evidence. If the process of making perceptual decisions is the same for humans as for monkeys, one would expect that the BOLD response would be higher for more difficult trials when responses are given in an RT condition, because more difficult trials demand more collection of evidence which in turn results in more summed neural activity (Figure 2). Kayser and colleagues reported results consistent with these predictions in a study using the RDM task (Kayser et al., 2010). The intraparietal sulcus (IPS) was reported to be

more activated for more difficult trials, and showed a correlation with the evidence from the sensory encoding in the MT+ region. The human homologues of the LIP-region in the rhesus macaque is the lateral intraparietal cortex region within in the IPS (Grefkes & Fink, 2005), thus making it a likely area involved in selection and preparation of eye-movement. The IPS showed similar activations in another RDM task where saccades were used to respond, but not for trials with button responses (Ho et al., 2009). Combining the results from the LIP activity in monkeys and the properties of fMRI one would expect a stronger BOLD response for easier trials in experiments with a forced delay between stimulus presentation and response (Figure 2). The DDM predicts that a decision boundary is reached earlier for easier trials, due to the higher accumulation rate. If the process is the same as for non-human primates, an accumulation area in the human brain should be active until a response is given, resulting in more integrated neural activity for easy than hard decisions. A part of the superior frontal sulcus (SFS) within the left DLPFC matched these predictions in a task where participants decided whether a noisy image contained a face or a house (Heekeren et al., 2004).
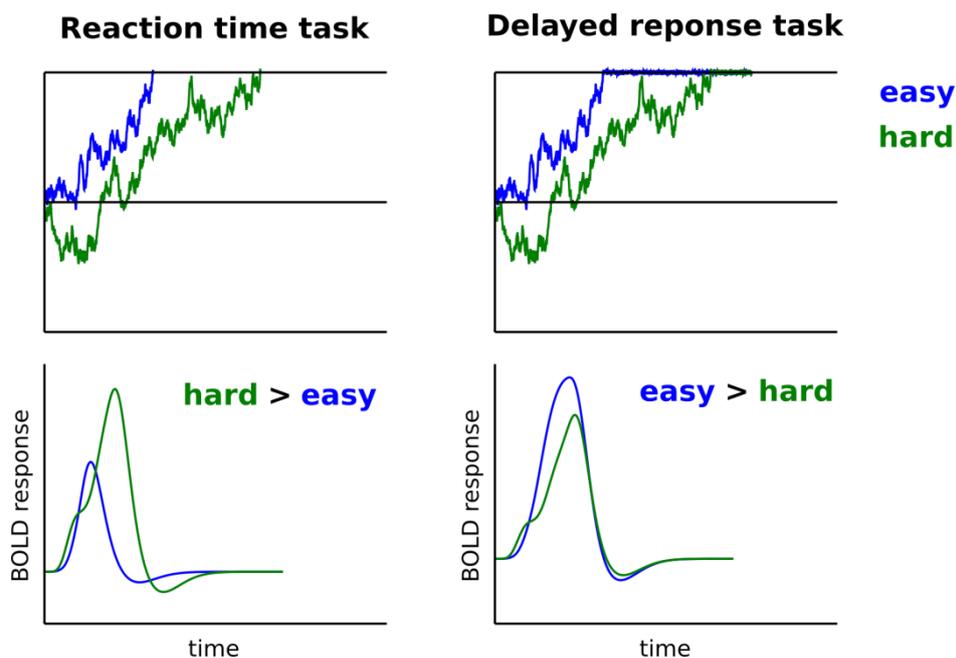
Figure 2. Predictions of BOLD-response of a potential accumulator region for easy and hard decisions in the reaction time (RT) condition, and the delayed response (DR) condition. The integrated neural response is assumed to be larger for hard decisions in a RT condition, and higher for easy decisions in a DR condition.

While the contrasts used for the two response conditions reported thus far were in line with what one would expect from an area in the human brain sharing the properties of the LIP region in monkeys; other studies have reported results which does not fit these predictions. For example, in an RDM task, Heekeren and colleagues (Heekeren, Marrett, Ruff, Bandettini

& Ungerleider, 2006) found activity in the same left SFS region previously reported for an easy larger hard contrast, but this time in a reaction time (RT) condition. Further, in value based decisions, activity in the IPS was more activated for harder trials in both an RT paradigm (Basten et al., 2010) and, along with the dorsomedial prefrontal cortex (DMPFC), in a delayed response (DR) paradigm (Hare et al., 2011). The ventromedial prefrontal cortex (VMPFC) has also been hypothesized to perform accumulation of evidence, as it has been shown to correlate with the ease of the decision in a value-based task using a DR condition (Rolls, Grabenhorst & Deco, 2010). Based on the differences in findings and their interpretations, it seems evident that researchers do not agree upon the defining criteria for accumulator regions. Table 1 summarizes some of the areas activated for different conditions in a selection of studies.

Table 1.

Overview of neuroimaging results.

| | Easy>Hard | | Hard>Easy | |
	RT	**DR**	**RT**	DR
Rolls et al. (2010)	X	**VMPFC**	**X**	X
Hare et al. (2011)	X	**VMPFC**	**X**	IPS, DMPFC, DLPFC
Heekeren et al. (2004)	X	**left SFS**	**X**	IPS, DMPFC
Heekeren et al. (2006)	left SFS, left IPL	**X**	**MPFC**	X
Basten et al. (2010)	left SFS, VMPFC	**X**	**IPS**	X
Kayser et al. (2010)	IPL	**X**	**IPS**	X
Ho et al. (2009)	left SFS*, left TPJ*	**X**	**IPS, MPFC, Insula**	X

Note. Regions activated for easy>hard and hard>easy contrasts across RT and DR conditions. Only areas of interest are reported. Marked with "X" are contrasts not performed or reported. The areas highlighted areas red are the regions that were reported to perform the accumulation of evidence. Areas marked with "*" were reported to be deactivated compared to baseline. The regions written in bold are the contrasts of interest based on the LIP activity in monkeys. IPL, inferior parietal lobule; MPFC, medial prefrontal cortex; TPJ, temporal parietal junction.

Aims of this study

The LIP region in macaque monkeys has been shown to increase its firing rate for easier tasks and to stay elevated after a threshold is reached, until a response is given

(Roitman & Shadlen, 2002). Although recent fMRI-studies have built on knowledge from neurophysiological research on non-human primates and the DDM, it remains unclear whether an accumulator region in the human brain shows the same properties as the monkeys' LIP region. The aim of this study is to directly test whether a region in the human brain shows these activations. This will be tested using a face-house perceptual decision task with two response conditions: one RT condition where responses are given as fast and accurately as possible; and one DR condition where responses are allowed only after a delay. To manipulate the difficulty level, the stimuli will have different degrees of noise. Using fMRI, the BOLD response of an accumulator region showing the same activations as the LIP in monkeys is expected to fulfill the following criteria: (1) a higher BOLD response for hard than easy trials in a reaction time (RT) condition, and (2) a higher BOLD response for easy than hard tasks in a delayed response (DR) condition (Figure 2). If any area shows the same activations as the LIP region in monkeys, it could be proposed that the process of making a simple perceptual decision is similar in monkeys and humans. If not, however, simple perceptual decision making mechanisms would be assumed to be different for non-human primates and humans.

Predictions. Based on the assumptions of the DDM, the accuracy is predicted to be higher for easy than hard decisions. In the RT condition, the response time is expected to be increased for more difficult decisions. A difference in response time is not expected in the DR condition as it is assumed that the decision boundary is reached before the cue to respond appears, thus removing the factor that results in different response times for easy and hard decision.

Sensory evidence is predicted to be coded in the FFA for faces and PPA for houses, as seen in Heekeren et al. (2004). These areas have been repeatedly shown to be activated for faces and places (Haxby et al., 1994; Kanwisher, McDermott & Chun, 1997). The activation in the FFA and PPA is expected to be correlated with difficulty level for their preferred stimulus type, with an increasing BOLD response for stimuli which are more easily identifiable. An accumulator region comparable to the LIP region in monkeys should show a higher BOLD response for hard trials in the RT condition and a higher BOLD response for easy trials in the DR condition. Based on previous literature we predict that an accumulation area should be found in an area comprising the left SFS, bilateral IPS, DMPFC, and VMPFC.

Methods

Participants

The study was approved by the Regional Ethical Committee of South-East Norway. All participants gave written informed consent, and were paid 200 NOK to participate. Twenty participants, 10 females, in the age range 23-40 (M = 29.36; SD = 6.16) took part in the study, recruited from the University of Oslo, and via acquaintances. They were all right-handed, and had normal or corrected-to-normal vision. Data from two participants were excluded from the analysis, leaving 18 participants (10 females); one due to technical difficulties, while another participant had a strong bias towards responding in favor of one of the alternatives, which resulted in overall accuracy and response times not comparable to the other participants.

Design

A two-alternative forced choice perceptual task with face and house stimuli was used. The independent variables were response condition and difficulty level, making the design a 2*2 factorial design. The dependent variables were accuracy, response times and BOLD response.

Setup

Creation of stimuli. The stimuli used were taken from a pool of 25 face images (face database, Max Planck Institute for Biological Cybernetics, http://faces.kyb.tuebingen.mpg.de/) and 25 house images (provided by Flavia Filimon) that were 131*156 pixels large, and subtended 5° degrees visual angle horizontally. A varying degree of noise was added to the pictures to manipulate difficulty. From each image, four images were created by adding different levels of noise, resulting in 100 unique face images and 100 unique house images. The four difficulty levels were grouped into two groups: easy and difficult (Figure 3), with different coherence levels for faces and houses (easy house: 51% and 54 % coherence; hard house: 43.7% and 46.5% coherence; easy face: 50% and 53% coherence; hard face: 42.7% and 44.5% coherence). The differences in coherence levels for the same difficulty level across stimulus type were used to better align accuracy of responses for house and face stimuli.
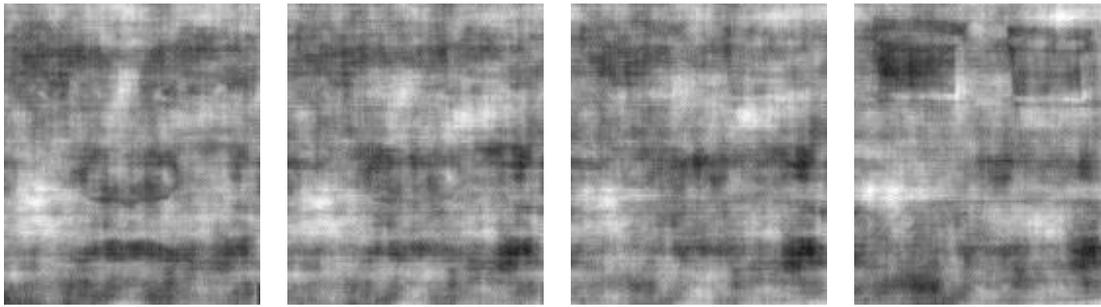
Figure 3. The stimuli were divided in the following categories (from left): easy face, hard face, hard house and easy house.

   Stimulus display. Participants performed a two-alternative forced-choice perceptual task, with face and house stimuli. There were two different response conditions (Figure 4): the reaction time (RT) condition and the delayed response (DR) condition, performed in separate runs. A trial in the two conditions was identical up to the presentation of the target stimulus. All stimuli were presented on a grey (RGB values: 127, 127, 127) background. Using a jittered event-related design, each trial started with the presentation of a white (RGB: 255, 255, 255) fixation cross, which was shown for between 2 and 9 seconds. Then, for 0.5 seconds, a red (RGB: 255, 0, 0) fixation cross was presented, to cue the participant to the upcoming task. After the red fixation cross, a scrambled image was presented for 0.5 seconds until the onset of the target image. The scrambled images were created by randomly scrambling tiles of 2 by 2 pixels from each of the 200 target stimuli. It was impossible to detect any information from these images, which were used as a baseline for the analysis of eye-tracking data, which was also recorded, to be used in a separate analysis. The target image was presented after the scrambled image. The target stimulus in each trial was chosen in a pseudo-random fashion for each participant, where it was made sure that a close to equal amount of face and house stimuli were presented in each run. In the RT condition, participants responded during the 1 second period the target stimulus was presented. Responses were given using left or right index finger, and the letters A (for "ansikt", face in Norwegian) and H (for "hus", house in Norwegian) were shown on either side of the screen, corresponding to the side used for responses for its alternative. The index finger used for each alternative was counterbalanced across participants. After the presentation of the target stimuli, the same scrambled image was presented for 0.5 seconds. In the DR condition, the target stimulus was presented for the same duration as in the RT condition (1 second), only without the letters on each side of the image. The scrambled iamge was presented for 1 second after the offset of the target image, but only during last 0.5 seconds of this period did the letters A and H appear on

each side of the image, which participants had been instructed beforehand to use as a cue to respond.
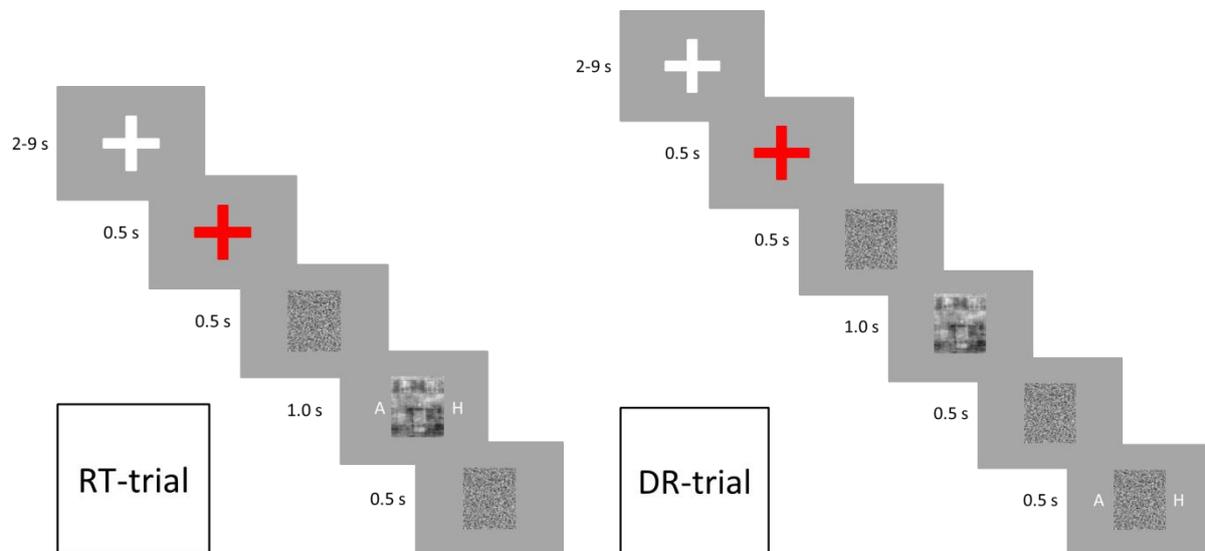

Figure 4. In the RT-trial, a white fixation cross (2-9 seconds) was followed by a red fixation cross (0.5 seconds) and the scrambled image (0.5 seconds) before the target stimulus was presented for 1 second. The letters on each side of the image indicated whether a left button press represented a face-response or a house-response. The letters disappeared as soon as a response was given, but the target stimulus stayed on for 1 second. After the target stimulus, the same scrambled image was presented for 0.5 seconds. The DR-trial was identical up to the presentation of the target stimulus. It was presented for 1 second in the DR condition as well, but the letters, informing the participant that a response could be given, were not presented until 0.5 seconds after the end of the presentation of the target stimulus. When the letters appeared, participants had 0.5 seconds to give a response.

In addition to the main experiment, a localizer task was used to localize the FFA and PPA area for each participant. To do this, a block-design with a 1-back task was used. Clear face and house images were presented in succession for 1,75 seconds with a 0.25 seconds long interval, consisting of a white fixation cross, presented between stimuli. The task was to respond whether the image currently presented was the same or different than the previous image. Face and house stimuli were presented in different blocks. This design was taken from Berman and colleagues (Berman et al., 2010).

While in the scanner, MR-compatible response grips were used to obtain responses (ResponseGrip®, NordicNeuroLab, Bergen, Norway), and the stimuli were presented using eye-tracking goggles with two LCD-displays (VisualSystems®, NordicNeuroLab, Bergen, Norway), both with a screen resolution of 800*600 pixels and refresh rate of 85 Hz. During training outside the scanner, stimuli were presented on a Dell laptop with a 15.6 inch screen, 1920*1080 pixels resolution and 60 Hz refresh rate, using keyboard buttons to respond. The

Presentation® software (Version 14.9, www.neurobs.com) was used to control the stimulus display and record responses.

Procedure

Prior to entering the scanner participants performed two runs of the RT condition and one run of the DR condition in a training session, each run consisting of 70 trials. The training was performed in a quiet room. The training session was used to prevent strong learning effects while in the scanner. Before a run started, information was presented on the screen about the response condition of run, and whether responses with left or right index finger represented face or house response. This information was also presented in the main experiment. After the training session, participants performed the main experiment in the scanner. The main experiment consisted of three runs, each consisting of 112 trials. The first and last runs were in the RT condition, and the middle run was in the DR condition. Each run lasted about 14 minutes and 17 seconds in the scanner. The localizer task followed the three runs of the main task. Before the task started, a screen appeared informing the participant about the objective of the task, and that left and right index finger represented a response for either yes or no. Each block consisted of 30 seconds of task followed by 15 seconds of rest, where a white fixation cross was presented. Blocks with face stimuli were followed by blocks with house stimuli, resulting in 5 blocks for each stimulus type.

fMRI Data Acquisition

For fMRI-data acquisition, a 3 Tesla Philips Achieva whole body MR scanner was used, with an 8-channel Philips SENSE head coil (Philips Medical Systems, Best, the Netherlands). A T2* echo-planar imaging sequence (repetition time (TR), 2250 ms; echo time (TE), 30 ms; FOV, 240*240*114; flip angle, 80°; interleaved acquisition) with 38 slices and a voxel size of 3*3*3 mm were taken while participants performed the task. One scanning session consisted of 381 volumes, taking approximately 14 minutes and 17 seconds. An additional 5 dummy scans were taken before the experiment started to allow the MR signal to reach equilibrium. After the three runs of the main task, participants performed the localizer-task, consisting of 209 volumes lasting about 7 minutes and 40 seconds. Anatomical T1 images with 170 slices and a voxel size of 1*1*1mm were recorded for registration of the functional images (TR, 6.6 ms; TE, 3.1 ms; FOV 256*256, flip angle, 8°).

fMRI Analysis

Data were analyzed using a mixed effects general linear model in FSL (www.fmrib.ox.ac.uk/fsl). The following preprocessing steps were taken: Motion correction using FMRIB's Linear Image Registration Tool (MCFLIRT), brain extraction using the Brain Extraction Tool (BET) function, spatial smoothing (with a Gaussian kernel of 5 mm full-width at half maximum), high-pass temporal filtering (>100 seconds) and slice timing correction. The design matrix of the General Linear Model (GLM) contained 8 explanatory variables of interest plus motion correction parameters and missed trials (4 % of all trials) as nuisance variables. The explanatory variables (EV) of interest were separated into correct and incorrect decisions for easy faces, easy houses, hard faces and hard houses. Stimulus duration was set to the reaction time (i.e. from onset of target stimulus until response) for each trial. The four explanatory variables containing error trials (7.5 % of all trials) were not included in the contrasts reported. Each subject's individual run was analyzed with a first-level analysis. Then, a second level analysis with fixed effects was performed to combine the three runs within participants. In the second-level analysis, the results from the RT and DR runs were contrasted. Finally, a third-level analysis was run using FMRIB's local analysis of mixed effect (FLAME1+2) with robust outlier detection. Z statistics images were cluster-threshold at Z > 2.3. Clusters with p<0.05 after correction for multiple comparisons (familywise error) in the regions of interest were reported as significant activations.

Data from the localizer-task were analyzed with face and house blocks as explanatory variables. These were contrasted against each other in the first level-analysis. The group mean of these results were computed in a higher-level mixed-effects (FLAME1+2) analysis. Clusters surviving a threshold of Z>2.3 with correction of multiple comparisons at p<0.05 were reported as significant.

<div align="center">Results</div>

Behavioral results

The DDM is a model that predicts changes in behavioral results following manipulations to stimuli or instructions. It is assumed that easier decisions should result in more correct responses and faster response times than harder decisions. However, because the decision boundaries were assumed to be reached before responding in the DR condition, the response times were not expected to be significantly different in the DR condition. Table 2 summarizes the behavioral results, which are in accordance with the predictions from the DDM. Due to the high accuracy across all conditions, the accuracy data was assumed to not

be normally distributed. Therefore, the Wilcoxon rank sum test was used to test for significance for the accuracy results. The response time results were tested for significance using the paired samples t-test. The accuracy was significantly higher for trials with a low compared to high degree of noise in both the RT condition (W(17)= 475, Z = 4.4780, p < 0.0001) and the DR condition (W(17)= 482.5, Z = 4.8302, p < 0.0001) (Figure 5a), while the response time was significantly increased for hard, compared to easy trials in the RT condition (t(17)= 8.393, p < 0.0001) (Figure 5b). The response times were higher for hard trials in the DR condition as well, but this difference was not significant (t(17)= 1.8427, p = 0.0829). It is therefore assumed that the threshold was reached before cued to respond in the DR condition. In the RT condition, there was a significant difference between response time for house and face responses (t(17)= 4.4381, p < 0.0001). This effect was perhaps caused by a bias towards responding face (Figure 5b). The difference was, however, not significant in terms of accuracy (W(17)= 370, Z = -1.1553, p = 0.248). Although the stimuli were the same for both RT and DR conditions, the mean accuracy was significantly higher in the DR condition (W(17)= 361.5, Z = 0.8859, p = 0.3757). The higher accuracy in the DR condition could be due to, in terms of the DDM, an increased distance between decision boundaries, thus decreasing the effect of noise. Another possibility is that the delay in the DR condition prevented motor-related errors, as many participants reported sometimes pushing the opposite button of what they intended. Although the difference in accuracy across difficulty level was bigger in the RT condition, it was not significantly bigger (W(17)= 356, Z = 0.7120, p = 0.4765).

Table 2.

Summary of behavioral results.

	Condition	Accuracy (IQR)	Response Time (SD)
Combined			
	Easy	96.8 (2.63)	967 (569)
	Hard	87.1 (6.02)	1022 (548)
RT			
	Easy	95.6 (3.86)	579 (101)
	Hard	85.3 (5.05)	646 (126)
	Easyface	97.6 (3.64)	551 (97)
	Easyhouse	93.7 (6.18)	607 (98)
	Hardface	86.8 (10.91)	625 (128)
	Hardhouse	83.8 (14.71)	667 (120)
DR			
	Easy	99.2 (1.79)	1773 (104)
	Hard	90.7 (7.05)	1781 (100)
	Easyface	99.5 (0)	1773 (105)
	Easyhouse	98.9 (0)	1773 (103)
	Hardface	89.8 (11.11)	1782 (100)
	Hardhouse	91.5 (14.81)	1780 (101)

Note. Accuracy is presented in mean percentage correct with interquartile range (IQR) in parentheses, while mean response times are shown in milliseconds with standard deviation (SD) in parentheses.
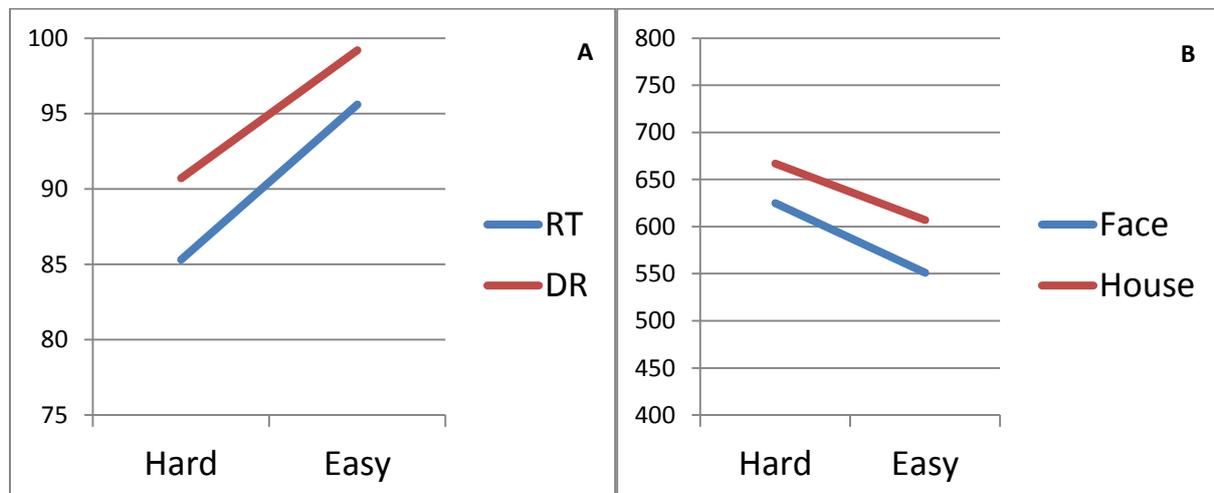

Figure 5. Differences in accuracy and response time. (**A**) The accuracy is shown in percentage correct for the hard and easy trials for both the RT and DR conditions. (**B**) The difference in response time in the RT condition across the two difficulty levels for face and house-stimuli.

Imaging results

Sensory evidence. Based on findings from previous studies (Kanwisher et al., 1997), it was expected that the FFA would be activated more for face stimuli than house stimuli, while the PPA was predicted to be more activated for house stimuli than for face stimuli. Further, these regions were expected to code sensory evidence by being more activated for stimuli

with less noise. To locate the face and house responsive regions, the results from the localizer-task were used to obtain a region of interest. As predicted, the FFA was more activated when seeing faces than houses. The opposite pattern was seen in the PPA (Figure 6 and Table 3). A region within the FFA was more activated for easy faces than hard faces, and a bilateral region within the PPA was more activated for easy houses than hard houses (Figure 6 and Table 3). Thus, these areas fulfilled the predictions of areas coding sensory evidence.
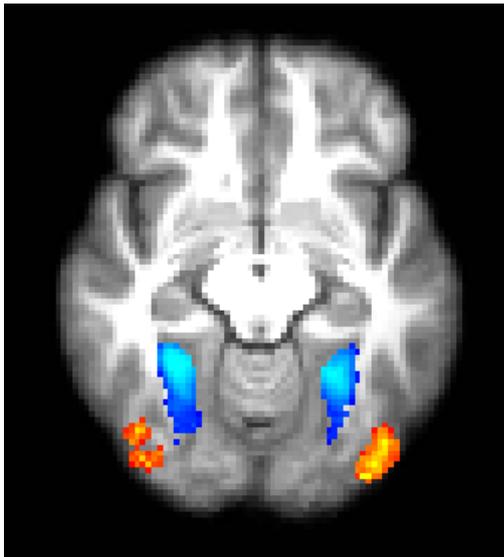

Figure 6. Activity in areas coding sensory evidence. Shown in blue is the contrast for house>face, while in red are face>house. Cluster threshold at Z>2.3. Activations are corrected for multiple comparisons at p < 0.05

Table 3.

Regions coding sensory evidence.

Contrast	Area	# of voxels	max Z-score	Peak voxel		
				X	Y	Z
House>Face						
	Right PPA	701	5.32	30	-48	-12
	Left PPA	520	5.11	-26	-50	-12
EasyHouse>HardHouse						
	Left PPA	114	3.16	-26	-48	-14
	Right PPA	84	3.08	24	-46	-16
Face>House						
	Left FFA	511	3.98	-38	-86	-12
	Right FFA	194	3.69	44	-72	-10
EasyFace>HardFace						
	Right FFA	41	3.02	36	-78	-16

Note. Activations found to be significantly active for house>face, easyhouse>hardhouse, face>house and easyface>hardface contrasts across RT and DR conditions. Peak voxel in Montreal Neurological Institute (MNI) coordinates. All activations are cluster threshold at Z>2.3, and corrected for multiple comparisons at p <0.05.

Accumulator region. Based on the results from neurophysiological studies, a region with the same properties as the LIP region in monkeys should be more activated for hard trials in the RT condition and easy trials in the DR condition. The data did not reveal any areas with this crossover interaction. However, based on the ROI analyses, comprising the DLPFC, VMPFC, DMPFC and IPS; the left IPS and the DMPFC were found to be significantly more activated for hard than for easy decisions across response conditions (Figure 7 and Table 4). These regions have previously been reported to be part of an accumulator process (Basten et al., 2010; Hare et al., 2011; Kayser et al., 2010). Figure 8 shows that these regions had a positive signal change for the hard>easy contrast for both the RT and DR condition. These regions were also positively activated compared to baseline for both difficulty levels in both conditions. This is a prerequisite of an accumulator area, which would be assumed to be more activated during task than rest.

Table 4.

Regions activated for difficulty-contrasts.

Contrast	Area	# of voxels	max Z-score	Peak voxel		
				X	Y	Z
Hard>Easy						
	DMPFC	1769	4.21	6	18	40
	Left IPS	372	3.97	-24	-68	32
Easy>Hard						
	Left IPL	691	3.81	-44	-68	34
	Right IPL	252	3.49	52	-62	30

Note. Areas showing a hard > easy and easy > hard contrasts for both conditions. Peak voxel in MNI coordinates. All activations are cluster-threshold at Z>2.3, and corrected for multiple comparisons at p < 0.05.
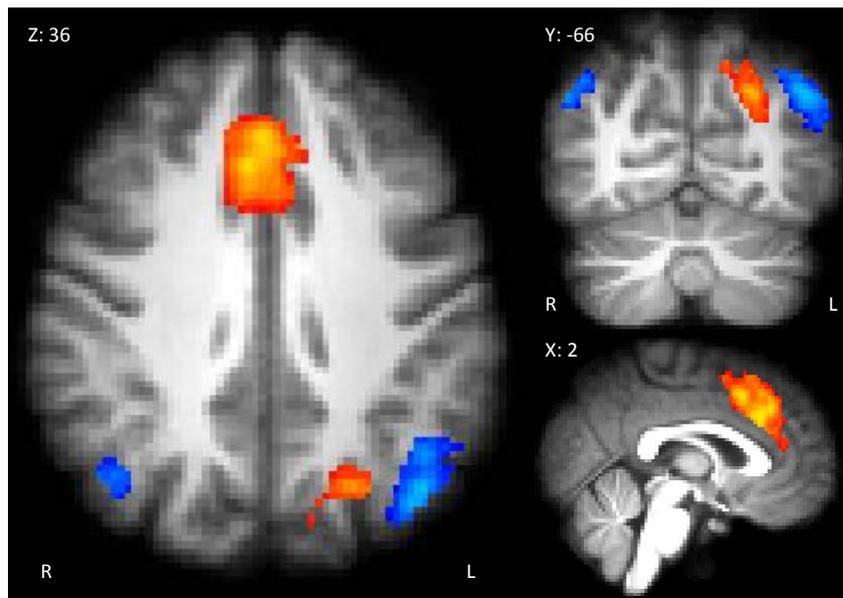
Figure 7. Shown in red are the results of the hard>easy contrast. Shown in blue are the results of the easy>hard contrast. Activations are cluster threshold at Z>2.3, and corrected for multiple comparisons at p <0.05.
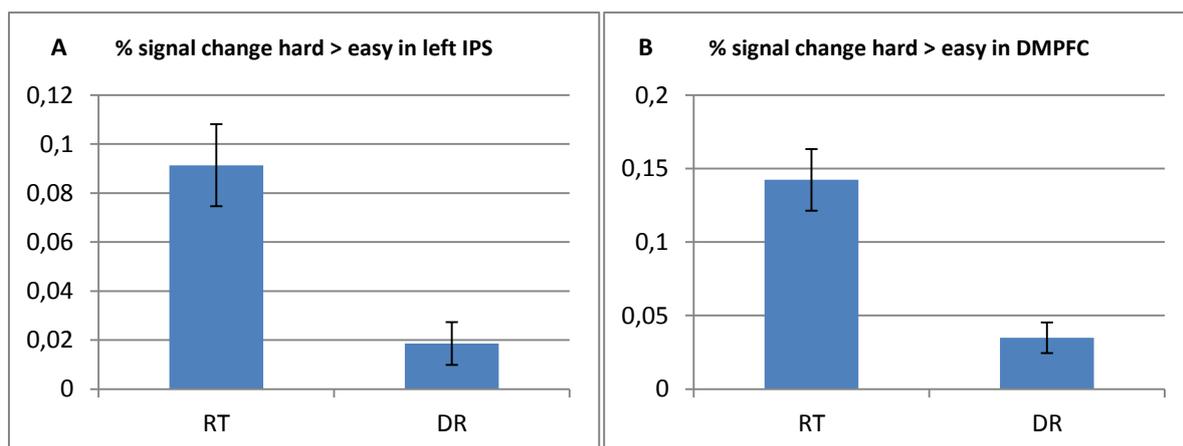

Figure 8. Percentage signal change for a hard>easy contrast for the RT and DR conditions for clusters within (**A**) the left IPS and (**B**) the DMPFC. Error bars represent ± 1 standard error across subjects.

Heekeren and colleagues (Heekeren et al., 2004; Heekeren et al., 2006) reported greater activation for easy>hard trials in the SFS, within the left DLPFC. These results were not replicated in the current study. The only area showing an increased activation for activation for easy compared to hard decisions in the regions of interest was in the bilateral inferior parietal lobule (IPL) region (Figure 7 and Table 4). This region showed the same pattern across response conditions (Figure 9), but it was found to be deactivated compared to baseline, and more strongly so for the harder decisions (Figure 10). An accumulator region would rather be expected to be positively activated compared to baseline, because the process of accumulating evidence presumably demands more neural activity than rest. The IPL is therefore assumed not to be a potential accumulator area.
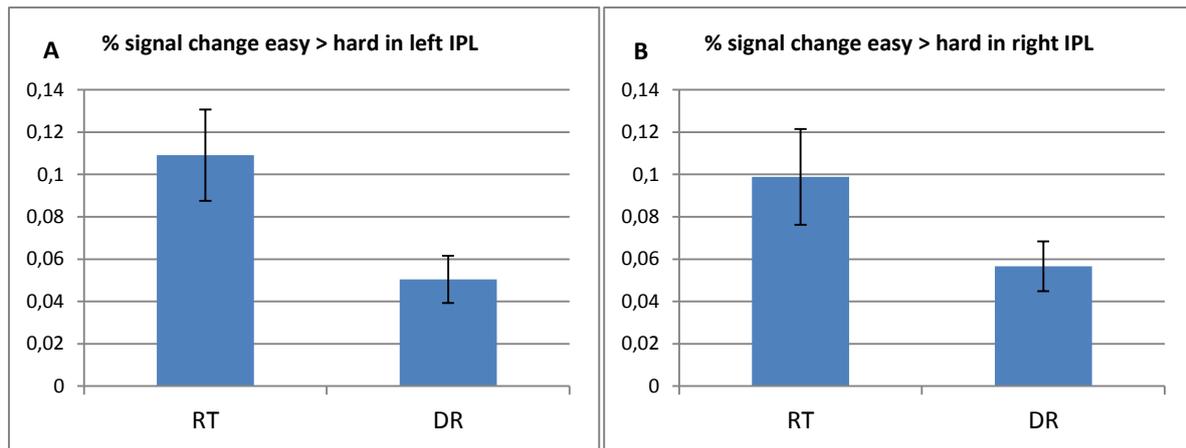
Figure 9. Percentage signal change for an easy>hard contrast for the RT and DR conditions for clusters within (**A**) the left and (**B**) right IPL. Error bars represent ± 1 standard error across subjects.
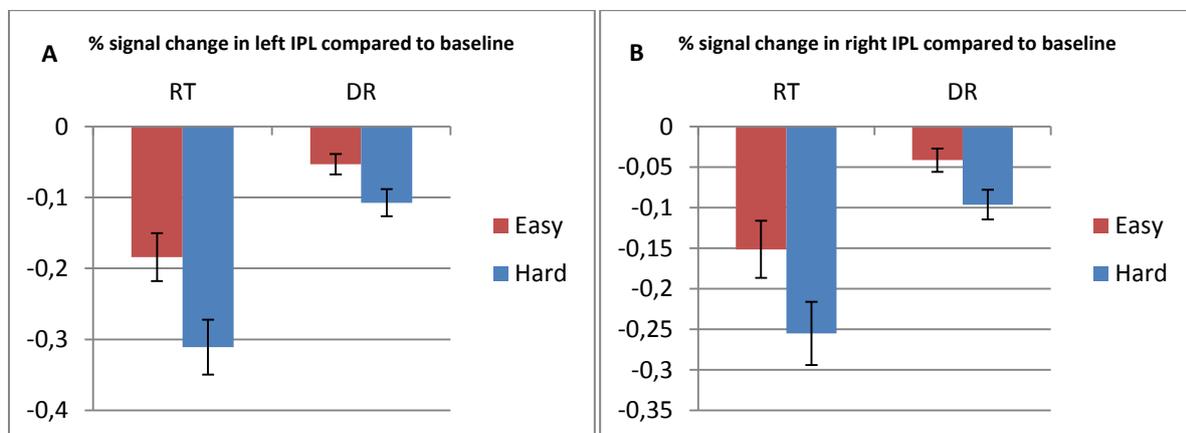

Figure 10. Percentage signal change for easy and hard decisions in (**A**) left and (**B**) right IPL compared to baseline in RT and DR conditions. Error bars represent ± 1 standard error across subjects.

Difference between response conditions. If the two response conditions would have close to identical activations, one could have argued that the conditions were too similar, thus explaining why an area with an interaction effect was not found. However, there were significant differences between conditions, both in the RT condition contrasted against the DR condition, and in the DR condition contrasted against the RT condition (Table 5). As can be seen in Figure 11, there were strong activations in the RT condition compared to the DR condition in temporal and occipital regions, most likely caused by the target image being presented throughout the trial. Also evident is greater activation in the IPS and DMPFC, which are active in this condition due to a stronger effect seen in the RT trials for both difficulty levels. Three regions were significantly activated more for the DR condition relative to the RT condition. The activity in the left lateral occipital cortex is close to the IPL region reported to be more activated for easy than hard decisions. This activation is due to the stronger deactivation compared to baseline in the RT condition (Figure 9a).

Table 5.

Activity for contrasts between response conditions.

Contrast	Area	# of voxels	max Z-score	Peak voxel X	Peak voxel Y	Peak voxel Z
RT>DR						
	Temporal, Occipital and Parietal Cortex	15161	9.48	24	-94	-10
	Cingulate Gyrus	1220	5.21	10	32	24
	Right Frontal Pole	1034	5.68	34	44	18
	Right Precentral Gyrus and Insula	495	6.13	46	4	18
	Left Insular Cortex	453	5.23	-26	26	-2
	Left Postcentral Gyrus	215	6.23	-44	-38	54
	Cingulate Gyrus	205	5.61	4	-34	22
DR>RT						
	Left Frontal Pole	388	4.58	-14	52	24
	Left Superior Frontal Gyrus	270	4.78	-22	30	32
	Left Lateral Occipital Cortex	268	5	-38	-70	32

Note. Areas activated for more between response conditions located with whole-brain analyses. Peak voxel in MNI coordinates. All activations are corrected for multiple comparisons at p<0.01, with a cluster threshold of Z>2.8.
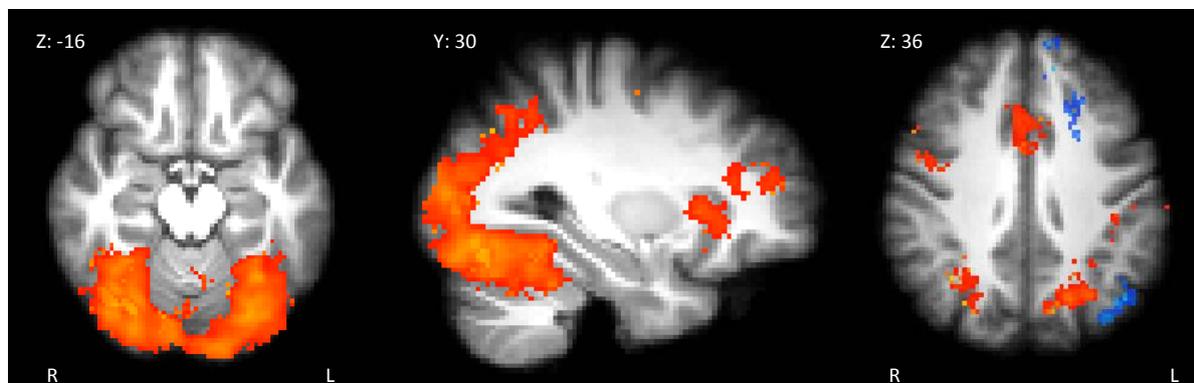

Figure 11. Regions in red had a stronger activation RT than DR conditions. Regions in blue were more activated for DR- than RT conditions. Activations are cluster threshold at Z>2.8, and corrected for multiple comparisons at p<0.01.

Discussion

This study has investigated whether an area in the human brain shows the same properties as an LIP region found to be accumulating evidence in the monkey brain during two-alternative forced choice tasks. For this aim, we used a simple perceptual decision making task with face and house stimuli. Categorizing the stimuli was either easy or hard, depending on the amount of noise added to the images. Two different response conditions

were used; one reaction time condition where responses were given as fast and accurate as possible, and one forced delay condition, where participants had to wait until after the presentation of stimuli before a response could be made.

In line with previous studies (Haxby et al., 1994; Kanwisher et al., 1997); areas within the FFA and PPA were found to be coding sensory evidence for faces and houses, respectively. The BOLD response of a region within the FFA increased more for easy than hard face stimuli. The same pattern was shown for house stimuli within the PPA. The results did not reveal a region with activations in line with the properties of accumulator neurons found in the LIP of monkeys. That is, no region had a crossover interaction with stronger activations for hard than easy trials in the RT condition and easy larger than hard in the DR condition. However, the DMPFC and left IPS showed similar activations across response conditions, with a stronger activation for hard relative to easy decisions. These regions have previously been reported to be involved in accumulation of evidence (e.g. Hare et al., 2011; Kayser et al., 2010). It thus seems likely that the process of accumulating evidence is different in monkeys and humans, and that humans might have evolved a decision making mechanism where the accumulation of evidence is separated from the maintenance of the decision. Some researchers hypothesize that an accumulator region should be activated more strongly for easier trials than hard ones. Activations for an in the areas proposed by those studies, including the left SFS and VMPFC (Heekeren et al., 2004; Heekeren et al., 2006; Rolls et al., 2010), were not found in this study. However, a bilateral region in the IPL was activated more strongly for easier decisions across response conditions. But, this region showed a deactivation compared to baseline for both difficulty levels, only less so for the easy decisions. A deactivation compared to baseline is not in line with the predictions of an accumulator region, thus the IPL is likely to play a different role.

Human decision making mechanism

Based on the results reported in the current study, and from other studies of decision making in humans, evidence suggest that the neural decision making mechanism for simple perceptual decision making is different for non-human primates and humans. The results from the neurophysiological studies suggest that the areas involved in planning the motor response both accumulates evidence and maintains the decision until the response is executed. These results suggest a type of embodied cognition (Wilson, 2002) where "to see and decide is, in effect, to plan a motor response" (Rorie & Newsome, 2005). However, the results from the current study suggest that the accumulation of evidence and maintenance of the decision is

not performed within the same area, since no region showed the crossover interaction in BOLD response that would be expected of such a process. Other studies performed on humans are in line with this distinction, where accumulator regions have been reported to be active across responses given with button pressing and saccades (Heekeren et al., 2006; Ho et al., 2009).

In a study by Tosoni, Galati, Romani and Corbetta (2008), the accumulation of evidence was reported to be performed in different areas when responses were obtained with hand pointing and saccade. Different areas in the posterior parietal cortex were reported to be more activated for easier trials for the two responses modes. This study used an extended delayed response condition, where the presentation of stimulus and response cue was separated by 10.5 seconds. Therefore, the areas within the posterior parietal cortex reported could be assumed to be the maintenance areas responsible for planning the motor response, and not the accumulation area. If receiving the decision from an accumulator region, these regions would be more strongly activated for easier trials, assuming the decision is received once a boundary is reached. Because the decision boundary is assumed to be reached earlier for easier decisions, this would result in maintaining the decision for a longer period of time for easier decisions.

The effects of difficulty level in the accumulator-areas reported in the current study were stronger in the RT than in the DR condition. This difference could have at least three potential causes. Firstly, it could be that the difficulty levels were perceived to be more similar in the DR condition, since the difference in accuracy between easy and hard trials was smaller within the DR condition. However, differences in proportion of correct responses were not significantly higher in the RT than the DR condition. Secondly, it could be that the effect was stronger in the RT condition because participants did twice as many trials in this condition compared to the DR condition, yet the effects showed the same pattern in an analysis using the same amount of trials for each condition. Finally, if the accumulation mechanism is active until a decision boundary is reached, but not longer, the difference in BOLD response to easy and hard decision could be diluted in the analysis of the DR condition. The BOLD response for each trial consisted of the period from stimulus onset until response, therefore the DR-trials would include the waiting period after decision boundaries are reached, when the accumulation process is finished. In the DR>RT contrast, one would thus expect to see regions responsible for maintaining the decision. The Neurosynth database (Yarkoni, Poldrack, Nichols, Van Essen & Wager, in press) was used to search for a candidate region of decision maintenance among the clusters found to be activated more in the DR than RT. The

terms "cue" and "delay" were reported to be involved for a coordinate (-28, 32, 32; MNI coordinates) within the left superior frontal gyrus cluster reported (neurosynth.org/locations/-28_32_32, retrieved 02.05.2012). These indications of a maintenance process are interesting, but will have to be investigated more thoroughly in order to conclude about the contributions of this region in the current study.

The idea of a general decision making mechanism, compared to a sensory-motor specific one, does seem to have certain advantages. Ho and colleagues (2009) made the argument that a general decision making mechanism demands less work load than a purely sensory-motor mechanism. Because a decision to act often needs several independent actions, e.g. when steering a bicycle to avoid a crash, a general decision making mechanism would be more efficient than if each motor region had to compute the decision independently. In the same article, a point is also made that monkeys in experiments may internalize the task they perform, considering that they perform the same task thousands of times during weeks or months. It could therefore be that the studies performed on humans and monkeys measure different types of decision making, where the human studies might have a higher ecological validity, and is closer to studying "natural" decision making.

Identifying accumulator activity

Researchers have used different BOLD-response contrasts in order to locate a potential accumulator-region. Some have proposed that the accumulator region should be more activated for easy than hard decisions (Heekeren et al., 2004; Heekeren et al., 2006; Rolls et al., 2010; Tosoni et al., 2008) while others assume the opposite (Basten et al., 2010; Hare et al., 2011; Ho et al., 2009; Kayser et al., 2010). The results in the current study support the assumption that an accumulator region should be more activated for hard decisions. First of all, because of the predictions of the DDM, it is assumed that evidence is gathered until a decision boundary is reached, and that this will result in a higher BOLD response for harder trials, because it measures integrated neural activity. Secondly, and based on the results from the current study, only one brain region showed an easy larger hard contrast across conditions, namely bilateral IPL. This region was however, deactivated compared to baseline for both difficulty levels, only less so for easy decisions. The TPJ area, close to the IPL region reported here, is part of the ventral attention network (Corbetta, Patel & Shulman, 2008; Posner & Petersen, 1990), which is involved in involuntary reorienting of attention. It is believed that this region can be deactivated by the dorsal attention network (Shulman et al., 2003), thought to be involved in voluntary reorienting during demanding tasks. Further, it is

assumed to be deactivated more for hard decisions because more time is spent to identify the stimulus (Ho et al., 2009). Ho and colleagues (2009) also reported this deactivation in the left TPJ, close to the IPL region found here. They also reported this effect for the left SFS, which has been proposed to perform the accumulation by Heekeren and colleagues (2004; 2006). The left SFS deactivation was also reported by Tosoni and colleagues (2008). In the current study, the left SFS did not show significant activations. With no significant activations in line with the predictions of an accumulator region for the easy larger hard contrast in the regions of interest, based on the ROI-analyses and whole-brain analyses, the current study supports the view that accumulator areas are more activated for harder decisions. The left IPS and the DMPFC showed this trend across response conditions. These areas have been consistently reported to be activated for this contrast (Basten et al., 2010; Hare et al., 2011; Ho et al., 2009), although not always thought to be part of decision making (Heekeren et al., 2004; Heekeren et al., 2006).

The IPS has been shown to be involved in categorization and identification of stimuli (Xu, 2009; Vogels, Sary, Dupont & Orban, 2002). It has been reported to be part of an accumulation process in several studies (e.g. Basten et al., 2010; Hare et al., 2011; Kayser et al., 2010). In a value-based decision making task (Basten et al., 2010), the IPS was shown to be negatively correlated with a comparison region, the VMPFC, and this effect was stronger for better decision makers, in addition to being more activated for harder trials. The IPS was also involved in another decision making study (Hare et al., 2011), where dynamic causal modeling (DCM; Friston, Harrison & Penny, 2003) was used to locate areas part of the process of making value-based decisions. In a RDM task (Kayser et al., 2010), using the psychophysiological interaction (PPI) analysis (Friston et al., 1997), the IPS was shown to interact with the sensory coding region of the MT+, and was negatively correlated with accumulation rate. A PPI analysis was also performed in the current study, where an attempt was made to find regions correlating with the absolute difference of the FFA and PPA activations, but this analysis did not yield significant results. The lack of significant results using the PPI analysis could be caused by the fact that the difference in difficulty (see behavioral results) was not large enough to find the effects reported in other studies.

The DMPFC was reported to be part of the decision making network reported by Hare and colleagues (2011), along with the IPS. In this study, the DMPFC-region was reported to have increased functional coupling at the time of decision with both the stimulus-value signal from VMPFC and left motor cortex during responses using the right hand and vice versa. The DMPFC has also been implicated in decision conflict (de Wit, Kosaki, Balleine & Dickinson,

2006; Mitchell et al., 2009), and comparison of decisions, being more activated during more difficult decisions (Venkatraman, Rosati, Taren & Huettel, 2009). Although assumed to be part of accumulation evidence, the current study does not allow a differentiation of the individual contributions of the IPS and DMPFC to this process.

<div align="center">**Limitations and future research**</div>

Modeling

      This study did not perform modeling of the behavioral data, but makes assumptions about the accumulation rate and the process of the model in general. It is assumed here, and found in other studies, that the rate of accumulation is negatively correlated with difficulty. It could be that the boundary separation was different in the RT and the DR condition, as indicated by higher accuracy in the DR condition. However, this would not undermine the conclusions, because the decision boundary is still believed to have been reached before the responses were made, supported by the fact that the response times were not significantly different for easy and hard decisions in the DR condition. There was also a significant difference in the mean response times for face and house stimuli in the RT condition. This could be caused by the starting point z being shifted towards the decision boundary of face responses, or that the face stimuli were easier to identify. Modeling of the behavioral data could clarify these issues.

Attention

      Attention is a possible confounding element when locating the accumulator region, because attention is assumed to be correlated with task difficulty. The regions reported here could therefore be attributed to attention processes. However, the studies showing connectivity from sensory and comparator regions, using PPI and DCM analysis, to the IPS and DMPFC (Basten et al., 2010; Hare et al., 2011; Kayser et al., 2010) provide support for processes other than attention. In a follow up study by Kayser and colleagues (Kayser, Erickson, Buchsbaum & D'Esposito, 2010), used RDM task where the task was either to report the direction of motion, or to decide which of the two colors the majority of dots had. The IPS was activated more for harder trials in both conditions, whereas other attention-areas were found to suppress information about movement of dots when the task was to decide about color. Ho and colleagues (2009) reported a delayed BOLD response onset in the IPS, which was thought to be a prerequisite for accumulator activity.

Conclusion

The results from the current study suggest that the mechanism of simple perceptual decision making is different in monkeys and humans. No area was activated in line with a crossover interaction with more activity for harder decisions in the RT condition and easier decisions in the DR condition. However, in keeping with previous studies, the IPS and DMPFC were activated more for harder decisions across response conditions, and were interpreted as accumulator-regions. A candidate region for maintaining the decision in the DR condition was found in the superior frontal gyrus. Future studies will have to investigate further the specific contributions of these areas in the process of simple decision making.

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