Prior Information Biases Stimulus Representations during Vibrotactile Decision Making

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Abstract

■ Neurophysiological data suggest that the integration of prior information and incoming sensory evidence represents the neural basis of the decision-making process. Here, we aimed to identify the brain structures involved in the integration of prior information about the average magnitude of a stimulus set and current sensory evidence. Specifically, we investigated whether prior average information already biases vibrotactile decision making during stimulus perception and maintenance before the comparison process. For this purpose, we used a vibrotactile delayed discrimination task and fMRI. At the behavioral level, participants showed the time-order effect. This psychophysical phenomenon has been shown to result from the influence of prior information on the perception of and the memory for currently presented stimuli. Similarly, the fMRI signal reflected the integration of prior information about the average vibration frequency and the currently presented vibration frequency. During stimulus encoding, the fMRI signal in primary and secondary somatosensory (S2) cortex, thalamus, and ventral premotor cortex mirrored an integration process. During stimulus maintenance, only a region in the intraparietal sulcus showed this modulation by prior average information. Importantly, the fMRI signal in S2 and intraparietal sulcus correlated with individual differences in the degree to which participants integrated prior average information. This strongly suggests that these two regions play a pivotal role in the integration process. Taken together, these results support the notion that the integration of current sensory and prior average information is a major feature of how the human brain perceives, remembers, and judges magnitude stimuli. ■

INTRODUCTION

The process by which information that is gathered from sensory systems is combined with prior information and used to influence how we behave in the world is referred to as *perceptual decision making* (Heekeren, Marrett, & Ungerleider, 2008; Gold & Shadlen, 2007). On a neural level, this is reflected by the integration and accumulation of sensory evidence about the different alternatives over time in specific brain regions (Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006; Huk & Shadlen, 2005; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Romo, Hernandez, & Zainos, 2004; Mazurek, Roitman, Ditterich, & Shadlen, 2003; Hernandez, Zainos, & Romo, 2002; Romo, Hernandez, Zainos, Lemus, & Brody, 2002). Theoretical accounts of perceptual decision making regard prior information as an essential ingredient in the decision-making process (Heekeren et al., 2008; Gold & Shadlen, 2007). It is still unknown, however, how and where in the brain prior information is integrated with current sensory evidence.

Prior information can affect the decision-making process at different levels. First, "priors" can directly influence the decision variable and bias the judgment process toward one of the alternatives. Until now, studies investigating the influence of prior information on the neural implementation of decision making only addressed this aspect and manipulated the probability (Basso & Wurtz, 1998; Carpenter & Williams, 1995) or the rewarded value (Sugrue, Corrado, & Newsome, 2004; Platt & Glimcher, 1999) of the alternatives. In addition, prior information could alter perception and memory by biasing the neural representation of sensory evidence toward more probable stimuli thereby affecting processes before the actual judgment. This aspect has not yet been addressed by neuroscientific research. Using delayed discrimination tasks, it is possible to disentangle the effect of prior information on the perception and maintenance of sensory evidence and judgment processes, respectively. Here, we investigated how and where in the brain prior information about the average magnitude of the stimulus set is integrated with current sensory evidence during stimulus perception and maintenance in a vibrotactile delayed discrimination task.

Psychophysical experiments investigating the delayed discrimination of magnitudes have found indirect evidence for an influence of prior average information on behavior (Hellström, 1985; Helson, 1964; Fechner, 1860). In these studies, subjects have to judge which of two stimuli differing in magnitude and separated by a short delay is of lower magnitude (Hellström, 2000, 2003; Sinclair & Burton, 1996;

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Baranski & Petrusic, 1992; Masin & Agostini, 1991). Consistently and independently of modality, these studies find an interaction between the stimulus magnitude and the time order of stimulus presentation, a phenomenon known as time-order effect. For low-magnitude stimuli, accuracy is high when the second stimulus is of lower magnitude than the first stimulus. Conversely, for high-magnitude stimuli, accuracy is high when the second stimulus is of higher magnitude than the first stimulus. Results of behavioral and modeling studies suggest that this behavioral pattern is a consequence of stimulus weighting processes and the effect of a general reference level which is determined by the stimulus set, context, and background information (Hellström, 1985; Helson, 1964). In more general terms, these weighting processes seem to reflect the integration of the currently presented stimulus and the average magnitude of the stimulus set, which is a learned representation about the average of the previous stimulus input. Because the time-order effect is a robust phenomenon in tasks of magnitude discrimination, we used it in the present study to investigate the effect of prior average information on perceptual decision making at a neural level.

The neural correlates of vibrotactile decision making have been studied intensively using single-unit recordings in monkeys (Lemus et al., 2007; Luna, Hernandez, Brody, & Romo, 2005; Romo et al., 2004; Brody, Hernandez, Zainos, & Romo, 2003; Romo, Hernandez, Zainos, & Salinas, 2003; Hernandez et al., 2002; Romo, Hernandez, Zainos, et al., 2002; Hernandez, Zainos, & Romo, 2000; Salinas, Hernandez, Zainos, & Romo, 2000; Romo, Brody, Hernandez, & Lemus, 1999) as well as neuroimaging and TMS studies in humans (Kostopoulos, Albanese, & Petrides, 2007; Li Hegner et al., 2007; Pleger et al., 2006; Preuschhof, Heekeren, Taskin, Schubert, & Villringer, 2006; Harris, Miniussi, Harris, & Diamond, 2002; Harris, Harris, & Diamond, 2001). The assumed chain of processes in the vibrotactile discrimination task involves encoding the first vibration frequency, maintaining this representation in working memory, and comparing this representation of the first stimulus with the representation second stimulus (see Figure 1). Whereas the primary somatosensory cortex (S1) represents sensory evidence provided by the vibrotactile stimuli and feeds this information to upstream areas, a distributed network including the secondary somatosensory cortex (S2) as well as the posterior parietal, prefrontal, and premotor cortices is active when sensory evidence has to be maintained during the delay period of the task. Activity in the same brain areas, especially in the ventral and medial premotor cortex (PMC), later mirrors the evolution of the comparison process. The time-order effect has already been observed in vibrotactile discrimination (Sinclair & Burton, 1996). This finding suggests that the effect of prior average information must be incorporated into the current model of vibrotactile decision making.

The mechanism by which the integration of prior average information leads to the behavioral pattern, reflecting the time-order effect, involves two stages. First, during stimulus encoding and maintenance, the representation of the first stimulus drifts toward the value of the average representation. Second, during stimulus comparison, the previous integration of current and average information affects the discriminability between the two stimulus representations differently for the two presentation orders. For example, considering low-magnitude stimuli (i.e., lower than the average of the stimulus set) and trials where the second stimulus is of higher magnitude than the first. In this case, the representation of the first stimulus drifts closer to the value of the second stimulus (which lies between the values of the first and the average). This decreases the distinctiveness between the two stimulus representations and leads to poorer performance. In contrast, in trials where the second stimulus is of lower magnitude than the first, the representation of the first stimulus drifts toward the average but away from the value of the second stimulus increasing the distinctiveness between the stimulus representations and improving performance. Importantly, the representation of average information seems to be sufficiently robust and stable after a relatively short learning phase (Morgan, Watamaniuk, & McKee, 2000). Morgan et al. (2000) compared two methods for measuring discrimination thresholds in which a test stimulus had to be compared with a standard stimulus. In one condition, in each trial the standard stimulus was presented before the test stimulus. In the other condition, only the test stimulus was presented and had to be compared against an internal standard, that is, an internal

Figure 1. Experimental design. Subjects placed the tip of their right index finger on a rubber disk glued to a piezoelectric wafer. Each trial began with a warning tone for 100 msec. Nine hundred milliseconds later, the first vibration was applied to the phalanx of the subjects' right index finger,

followed by a delay of 100 or 4100 msec. After the delay, the second vibration was applied to the same finger. The subjects had to decide whether the second vibration had a higher or a lower vibration frequency than the first vibration and indicated their choice by pressing one of two response buttons with their left index or middle finger. The first vibration had one of six different vibration frequencies (16, 20, 24, 28, 32, and 36 Hz). The second vibration was either 3 Hz higher (50% of the trials) or lower than the first vibration.
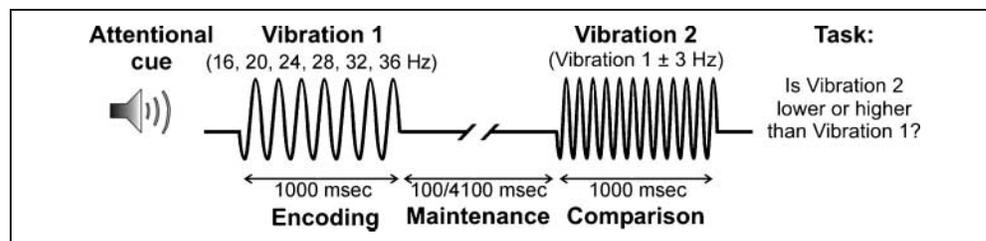
representation of the average of the stimulus set. Discrimination accuracy in the internal standard condition improves over the first 15 to 20 trials of the experiment. After that, subjects can maintain a steady representation of the internal standard stimulus and use this internal standard with the same accuracy as an external standard. These results suggest that subjects quickly develop a robust, internal, long-term representation of the average value of a stimulus set that affects their performance during the remainder of the experiment.

In the present study, we used fMRI and a paradigm known to produce the time-order effect to investigate the neural mechanism reflecting the integration of average information and current sensory evidence during the encoding and maintenance period of the vibrotactile delayed discrimination task. Our main question was, which brain regions are related to the integration of the first vibrotactile frequency with the average frequency before the second vibrotactile stimulus is presented? If there are brain regions that integrate the difference between these two representations, the BOLD signal should reflect this integration process. Prior information has a neural representation (Summerfield & Koechlin, 2008). One possible neural mechanism for the integration of prior information is that neural activity of brain regions related to the encoding and maintenance of vibrotactile frequencies is biased toward the value of the average vibration frequency. Specifically, we hypothesized that these brain regions integrate both pieces of information—prior information and current sensory evidence—by encoding the difference between the two representations during the encoding and the maintenance of the first vibrotactile stimulus. The neural activity in these brain regions should, therefore, reflect the difference between the current vibration frequency and the average vibration frequency; it should increase with increasing difference between prior information and current sensory evidence (Heekeren et al., 2008; Gold & Shadlen, 2007; Romo & Salinas, 2003). As a consequence, the BOLD signal, which is an indicator of neuronal activity (Logothetis, 2008), should be greater with increasing distance. Importantly, if a brain region is crucially involved in the integration of prior average information, interindividual differences in brain activity should mirror the degree to which individual subjects incorporate prior average information into their representation of the current vibration frequency. Consequently, the second question was, do changes in the brain regions related to the assumed integration process correlate with the subsequent behavior displayed by the individual subjects?

METHODS

Subjects, Task, Data Acquisition

The 20 subjects, experimental procedure, and stimuli of this study have been described previously in more detail (Preuschhof et al., 2006). Two vibrotactile stimuli differing in vibration frequency and separated by an ISI of 100 or 4100 msec were applied sequentially to the distal phalanx of the right index finger (Figure 1). In each trial, the frequency of the first vibration (16, 20, 24, 28, 32, or 36 Hz) varied randomly. The second vibration was either 3 Hz higher or lower than the frequency of the first vibration. Subjects had to indicate by left hand button presses which of the two vibrations had the higher vibration frequency.

Imaging was conducted on a 1.5-T Magnetom Sonata MRI system (Siemens, Erlangen, Germany) equipped with a standard head coil. A vacuum pad was used to minimize head motion. Functional images were acquired using a BOLD-sensitive T2*-weighted EPI sequence (repetition time = 2500 msec; echo time = 40 msec; flip angle = 90°; field of view = 256 mm; matrix = 64 × 64 mm; 26 axial slices positioned parallel to the bicommissural plane; slice thickness = 4 mm; interleaved acquisition). Per subject, we acquired two to three functional runs in which the subjects performed the vibrotactile discrimination task. Each run lasted 8 min 45 sec and contained 24 short ISI as well as 24 long ISI trials. One third of the scanning time consisted of null events that were randomly inserted between trials. Trial onsets were jittered in steps of 0.5 repetition time (500 msec). The intertrial interval varied from 0.5 to 17.5 sec (mean = 4 sec). The temporal sequence of the trials in each run was optimized and pseudorandomized using Optseq2 (http://surfer.nmr.mgh.harvard.edu/optseq). The first two scans of each run were discarded to allow longitudinal magnetization to reach equilibrium. Immediately before the fMRI experiment, participants performed a practice session containing 48 trials. The stimulus range and the mean were the same for the practice session and the fMRI experiment. Therefore, the subjects already knew the stimulus distribution and were able to develop an internal representation of the average vibration frequency before the beginning of the fMRI experiment.

Behavioral Data Analysis

Behavioral data were analyzed using SPSS (Version 14.0; SPSS Inc., Cary, NC). To test whether participants used prior average information and combined it with the information about the first vibration frequency, we assessed the time-order effect by computing accuracy in relative frequency of correct responses and RT of correct responses in milliseconds. This was done separately for each frequency value of the first vibration, time order of presentation (i.e., first or second frequency higher), length of ISI, and subject. Repeated measures analyses of variance with the within-subject factors frequency of first vibration, presentation order, and ISI as well as the random factor subjects were conducted on RT and accuracy.

To evaluate whether the representation of the average frequency develops during the practice session and is already present at the end of the practice session, we calculated the time-order effect for the first and the last trial of practice

session for each possible pair of vibration frequencies as an average over all subjects. To assess whether the time-order effect changes during the fMRI experiment, we also compared the behavioral pattern for the first and for the second half of the fMRI experiment.

fMRI Data Analysis

MRI data were analyzed with SPM2 (http://www.fil.ion.ucl.ac.uk/spm/software/spm2). Preprocessing of the data was performed before statistical evaluation. First, slice timing differences due to acquisition order were adjusted. Parameters for motion artifacts were determined using six parameters for rigid body transformation and translation. The first image of the first run was normalized to the MNI EPI template. The parameters from this normalization and the motion correction were applied to all functional images. Finally, data were spatially smoothed using a three-dimensional Gaussian filter of 8-mm FWHM.

Voxel-based statistical analysis was based on the general linear model (Friston et al., 1995). Low-frequency drifts were removed using a temporal high-pass filter (cutoff = 128 sec) and intrinsic autocorrelations were modeled. Design matrices were generated using event-related regressors and then convolved with a canonical hemodynamic response function.

We specified a model consisting of six regressors. Three of these six regressors represented the encoding, the maintenance, and the comparison period of the task, respectively. The regressor for *encoding* comprised the duration of the first vibration and lasted 1 sec. The regressor for *maintenance* started 100 msec after the end of the first vibration and lasted 4 sec. The regressor for the *comparison* period started with the beginning of the second vibration and lasted 1.5 sec, including the subject's response. Whereas the regressor for maintenance included only the 4-sec long maintenance period of the trials with the long ISIs, the regressors for the encoding and comparison period incorporated trials with short and long ISIs.

To determine the influence of prior average information on brain activity in the three task periods of the vibrotactile delayed discrimination task, we additionally specified parametric modulations of these three regressors: the encoding integration regressor, the maintenance integration regressor, and the difficulty regressor.

The integration of average information with current sensory evidence provided by the first vibration stimulus may take place both during the encoding and maintenance period. The integration process should already start during the encoding period while the first vibrotactile stimulus is present. The integration process should continue during the maintenance period while subjects try to maintain the first vibration frequency. In both the encoding and the maintenance period, the neural representation of the vibration frequency is assumed to drift toward the value of the average vibration frequency. Therefore, for

the encoding and the maintenance regressors, we defined parametric modulations representing the activity of brain regions related to the integration of the first vibration frequency of a trial with the average frequency of the entire stimulus set. The integration process should be stronger with increasing difference between the frequency of the first vibration stimulus and the average frequency. Therefore, the values of these parametric modulations were obtained in the following way: We calculated the absolute value of the difference between the first vibration frequency and the arithmetic mean of the stimulus set (26 Hz). This resulted in three different values (2, 6, or 10) for the six different frequencies. Higher values reflect larger deviations of the first vibration frequency from the mean thereby modeling the integration process.

The integration of average information should affect the difficulty of the discrimination. Discriminations should be easier when the frequency of the first vibration lies between the frequency of the average and the frequency of the second vibration. In this case, the neural representation of the first vibration drifts toward the average frequency and away from the value of the second stimulus, making the discrimination easier. This is the case for low-magnitude stimuli when the second vibrotactile stimulus has a lower frequency than the first stimulus and for high-magnitude stimuli when the second vibrotactile stimulus has a higher frequency than the first stimulus (preferred time order). Decisions should be more difficult when the second vibration lies between the first and the average vibration. In this case, the neural representation of the first stimulus drifts toward both the value of the average and the value of the second stimulus rendering the task more difficult. This is the case for low-magnitude stimuli when the second vibration has a higher frequency than the first vibration and for high-magnitude stimuli when the second vibration has a lower frequency than the first vibration (unpreferred time order). Therefore, a parametric modulation was defined for the comparison period to indicate brain regions related to the difficulty of the decision. The values of this "difficulty regressor" were calculated using the following procedure. First, the absolute value of the difference between the second vibration frequency and the arithmetic mean of the stimulus set was computed. Second, the sign of these values was set positive for the unpreferred time order and set negative for the preferred time order of stimulation. The resulting values (-13, -9, -5, -1, 3, 7) defined the parametric modulation of the comparison regressor. In total, the resulting design matrix was composed of six regressors.

Contrast images were computed for all regressors and for each subject using t statistics. Group activation maps for each regressor were computed with the subject-level contrast images using simple t tests. The significance threshold for these random-effects analyses was set to $t \geq 3.58$ ($p < .001$; uncorrected for multiple comparisons).

In addition, we tested whether the individual BOLD signal in brain regions that were associated with the assumed

integration process also reflected interindividual differences in the magnitude of the time-order effect. For this purpose, we computed a behavioral value reflecting the magnitude of the time-order effect and then used it in an fMRI regression analysis. For the individual subjects, we fitted a linear function to the accuracy values for the six frequency values of the first vibration in a trial. This was done separately for the two presentation orders and the two ISI conditions. The estimated b values characterize the slope of the curve and therefore indicate the individual magnitude of the time-order effect across subjects. Because the curves for the presentation condition "second stimulus lower" have a negative slope, we multiplied those b values with -1 for this condition. We then averaged the b values for the two presentation conditions and the two ISI conditions, resulting in three behavioral values for each subject: one for the short ISI trials, one for the long ISI trials, and one representing all trials.

We then defined functional ROIs for which the BOLD signal was parametrically modulated by the difference between the average and the first vibration frequency for the encoding and for the maintenance period, respectively. For this purpose, we thresholded the respective t maps of the first whole brain analysis using a significance level of $p < .005$ (uncorrected for multiple comparisons). For these functional ROIs, we computed a simple regression (correlation) as implemented in SPM2 using the individual contrast images related to the integration regressors and the corresponding individual behavioral values. For the analysis related to the encoding period, we used the contrast images related to the encoding integration regressor (which comprises the trials with short and long ISI) and the individual behavioral values averaged over all trials. For the correlation analysis related to the delay period, we used the contrast images related to the maintenance integration regressor (which only includes trials with long ISI) and the behavioral values related to the long ISI trials only. The significance threshold for correlation analyses was set to $t \geq 1.73$ ($p < .05$; uncorrected for multiple comparisons).

To illustrate the temporal evolution of the BOLD signal in the significantly activated clusters, we computed time courses for the hemodynamic responses using MarsBaR 0.38 (https://sourceforge.net/projects/marsbar). For each subject, we computed finite impulse response models for the clusters that were significantly activated in relation to the parametric regressors (the encoding integration regressor, the maintenance integration regressor, and the difficulty regressor, respectively). A first model was computed to extract the time courses related to the integration process. This model incorporated only the trials with the long ISIs. Time courses were extracted separately for the three different trial types corresponding to the values of the integration regressors. To extract time courses related to the difficulty regressor, we specified a different model . Here, six different trials were incorporated corresponding to the values of the difficulty regressor. In both models, only trials with long ISIs were incorporated starting with the onset of the tone and lasting 6.5 sec. Percent signal change was estimated at each of 10 time points with an interval of 2.5 sec ranging from trial onset to 25 sec posttrial.

RESULTS

Behavioral Data

Behavioral results revealed the expected interaction between the magnitude of the first vibration frequency and the time order of presentation, $F(5,95) = 23.9$, $p < .001$, providing evidence for an effect of prior information on vibrotactile decision making. Performance was better for low magnitudes when the second vibration frequency was lower than the first and worse when the second frequency was higher than the first (see Figure 2). The reverse relationship was found for high-magnitude stimuli. In addition, we found a three-way interaction between the factors magnitude of the first vibration frequency, time order of presentation, and ISI, $F(5,95) = 6.6$, $p < .001$,

Figure 2. Time-order effect. Interaction between the magnitude of the first vibrotactile stimulus of a trial and the time order of presentation. Left panel, accuracy: better performance for low magnitudes when the second vibration was lower than the first vibration (preferred time order) and worse performance when the second vibration was higher than the first vibration (unpreferred time order). Reverse relationship for high-magnitude stimuli. Right panel, RTs: lower RT for low magnitudes when the second vibration was lower than the first vibration (preferred time order) and higher RT when the second vibration was higher than the first vibration (unpreferred time order). The reverse relationship was found for high-magnitude stimuli.
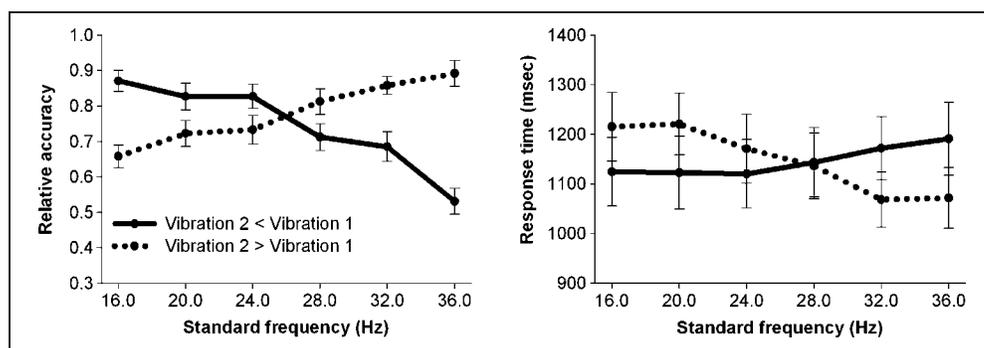
indicating the size of time-order effect increases with increasing ISI. For RT, the pattern was inverted, $F(5,95) = 6.2, p < .001$, with lower RTs for low magnitudes when the second frequency was lower than the first frequency and higher RTs when the second frequency was higher than the first. As for accuracy, the reverse relationship was found for high-magnitude stimuli. On RT, we also found a three-way interaction between the factors magnitude of the first vibration frequency, time order of presentation, and ISI, $F(5,95) = 3.3, p < .005$.

Figure 3 (left) shows that the time-order effect was present in the last quarter but not in the first quarter of the practice session. Figure 3 (right) shows that the magnitude of time-order effect did not differ between both halves of the fMRI experiment. These analyses indicate that the time-order effect already developed during the practice session and remained stable during the course of the fMRI experiment. Behavioral studies in non-human primates indicate that the representation of prior information is most heavily influenced by the most recent trials (Sugrue, Corrado, & Newsome, 2005). In these studies, behavioral success depends on the animal's ability to identify the changing values of the different response options by analyzing their reward history. Therefore, optimal performance requires fast updating of the representation of relative values of the response options according to the changing input statistics. By contrast, in our study, all response options were equal and stimulus-response associations did not change during the experiment. It has been suggested that noisy sensory evidence about the current vibration frequency is combined with long-term knowledge about the average vibration frequency to enhance the fidelity of the stimulus representation and improve performance (Hellström, 1985). The updating of the representation of the average magnitude of the stimulus set does not occur on a trial-to-trial basis but on a longer time scale. We therefore assume that, similar to previous observations regarding the development of internal standards (Morgan et al., 2000), for our task the rep-

resentation of the prior information is more robust and longer lasting than in reward experiments.

fMRI Data

The observed behavioral pattern indicates that information about the average vibration frequency plays an important role in task performance. Next, we wanted to get more conclusive evidence about the assumption that sensory evidence provided by the first vibrotactile stimulus is integrated with information about the average frequency during the encoding and the maintenance period of the task. For this purpose, we used the fMRI data and identified brain regions in which the BOLD signal reflects such an integration process. To ascertain which brain regions are involved in the process of stimulus integration during encoding and maintenance period, we separately defined the parametric modulations related to the encoding (encoding integration regressor) and the maintenance (maintenance integration regressor) period of the task. To identify brain regions related to the difficulty of the decision, we defined another parametric regressor for the comparison period (difficulty regressor). The complete model comprised a total of six regressors. Three regressors represented the three periods of the vibrotactile delayed discrimination task: encoding, maintenance, and comparison. In addition, the model included parametric modulations of these regressors: the encoding integration regressor, the maintenance integration regressor, and the difficulty regressor for the comparison period of the task.

The regressors for encoding, maintenance, and comparison were associated with an increased BOLD signal in a network of brain regions that has previously been described for the vibrotactile delayed discrimination task (Kostopoulos et al., 2007; Li Hegner et al., 2007; Pleger et al., 2006; Preuschhof et al., 2006). The focus of this article is the analysis of the effects related to the parametric regressors reflecting the distance between the vibrotactile

Figure 3. Development and stability of the time-order effect. The left panel shows the accuracy for the first and the last trial for each possible vibration pair of the practice session (average over all subjects), indicating that the time-order effect developed during the practice session. The right panel shows the accuracy for the different vibration pairs for the first and the second half of the fMRI experiment (average over all subjects), indicating that the effect remained stable during the entire fMRI experiment.
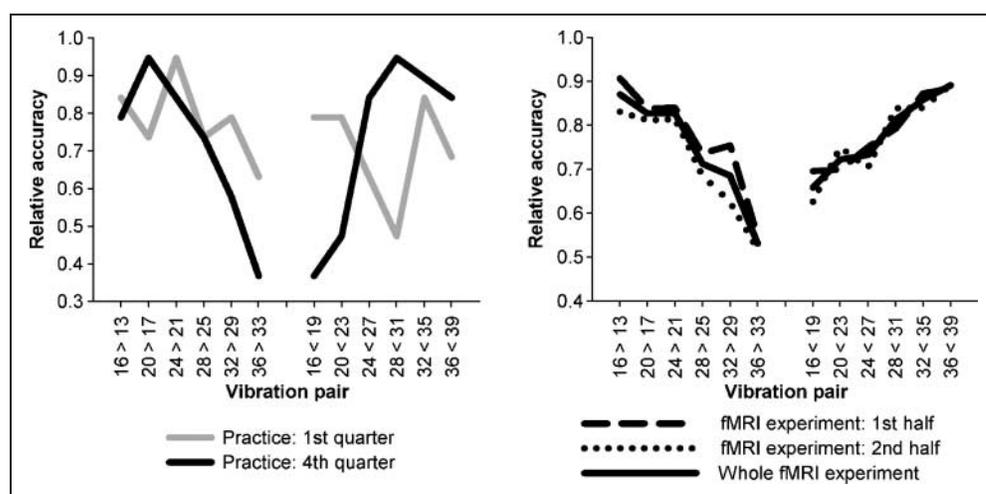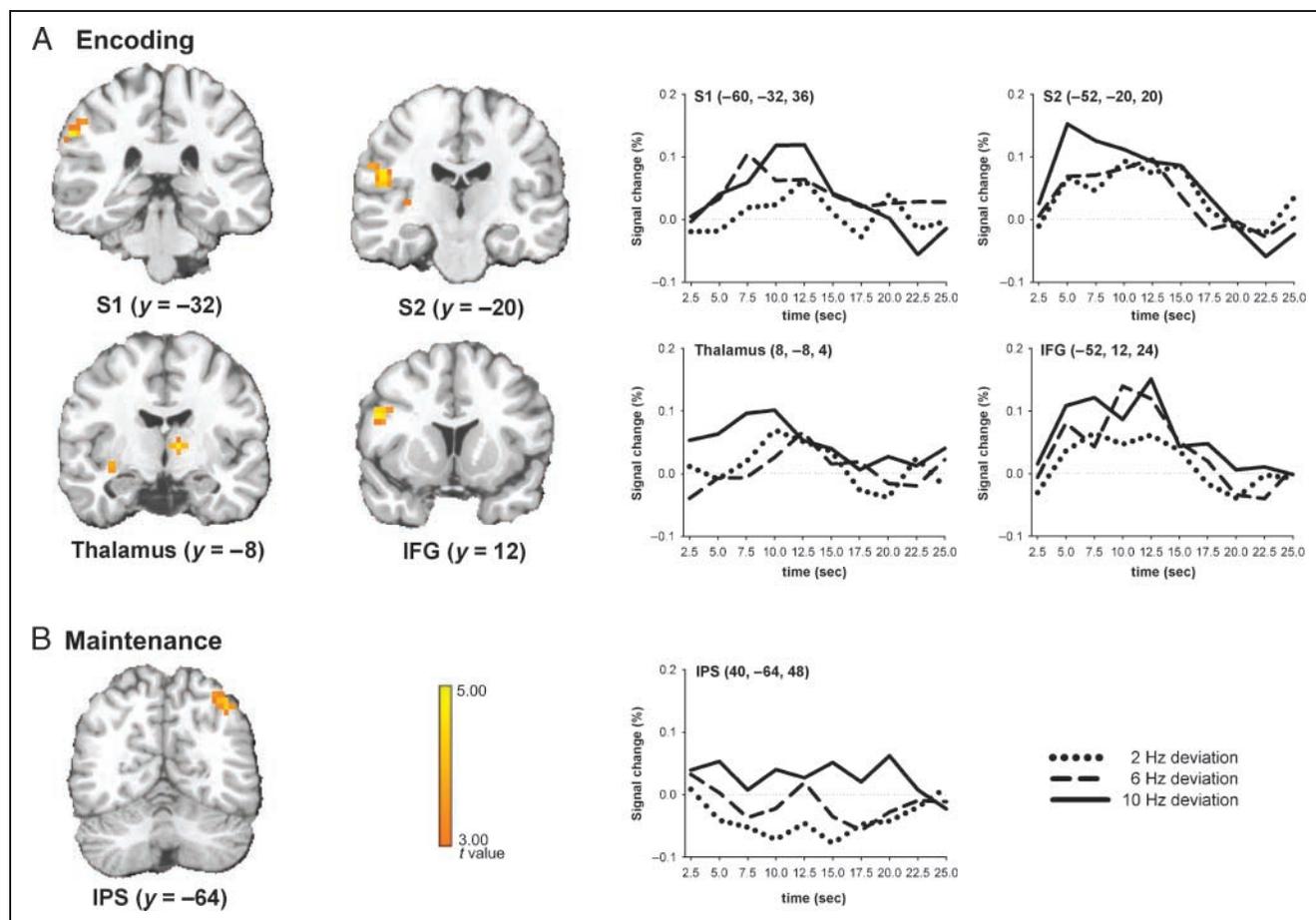
Figure 4. Neural correlates of the integration of average information and current sensory evidence. Brain regions in which the BOLD signal reflects the difference between values of the first vibration frequency and the average frequency (left panel) and the corresponding time courses estimated from the corresponding activation clusters (right panel). (A) During encoding. (B) During maintenance. Activation clusters (shown at $p < .003$, uncorrected) are projected on the MNI template "Colin." S1 = primary somatosensory cortex; S2 = secondary somatosensory cortex; IFG = inferior frontal gyrus; IPS, intraparietal sulcus.

frequency stimuli of a trial and the average frequency of the entire stimulus set. Therefore, we will only report activation related to the parametric regressors.

First, we identified brain regions related to the integration of the first vibration stimulus with the average frequency before the comparison period. During the encoding period, the BOLD signal in S1 and S2, the thalamus, and the ventral PMC covaried with the difference between the average frequency and the first vibration (see Figure 4A and Table 1). During the maintenance period,

Table 1. Anatomical Locations and MNI Coordinates for the Parametric Regressors Related to Encoding, Maintenance, and Comparison

Condition	Anatomical Region	BA	Hemisphere	MNI Coordinates			Voxel t Value (z Value)
				x	*y*	*z*	
Encoding	Postcentral G (S1)	2	L	−60	−32	36	4.94 (3.92)
	IFG	44	L	−52	12	24	4.88 (3.88)
	Thalamus		R	8	−8	4	4.78 (3.83)
	OP 1 (S2)	43	L	−52	−20	20	4.64 (3.75)
Maintenance	IPS	7	R	40	−64	48	4.36 (3.59)
Comparison	ACC	32	R	4	32	28	3.98 (3.35)

$p < .001$. Abbreviations: G = gyrus; IFG = inferior frontal gyrus; IPS = intraparietal sulcus; OP = operculum; S1 = primary somatosensory cortex; S2 = secondary somatosensory cortex.
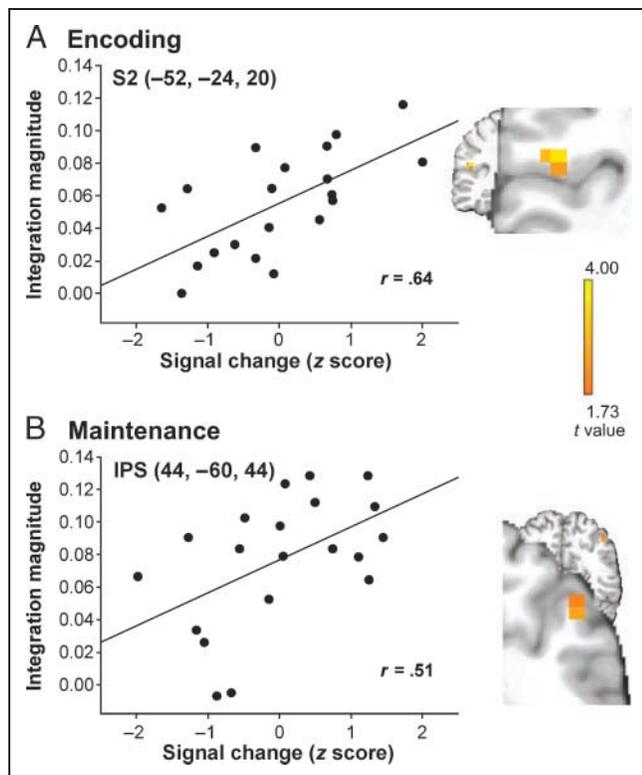
Figure 5. Correlation between the individual magnitude of the time-order effect and brain activity. The BOLD signal in S2 and IPS reflects interindividual differences in the relative weight of the average information on the current stimulus representation. (A) Encoding activity in S2 is associated with individual differences in the integration of the prior vibration frequency, whereas (B) activity in the IPS is associated with the integration of prior information during maintenance. The calculation of the individual integration magnitudes is described in the Methods section. Activation clusters (shown at $p < .05$, uncorrected) are projected on the MNI template "Colin." S2 = secondary somatosensory cortex; IPS = intraparietal sulcus.

only the BOLD signal in the intraparietal sulcus (IPS) co-varied with this difference (see Figure 4B and Table 1).

Second, we assessed in which of these five brain regions the BOLD signal is correlated with interindividual differences in the degree to which subjects rely on prior average information relative to current sensory evidence provided by the first vibration. Specifically, we tried to identify the regions where the beta weights of the parametric regressors for the encoding and the delay period covaried with the individual magnitude of the time-order effect. These correlation analyses revealed that the BOLD signal in S2 during the encoding period and in the IPS during the maintenance period correlated with the individual behavior (see Figure 5): Individuals who showed a greater BOLD signal change related to the deviation of the first vibration frequency from the average frequency seemed to weight the average information more strongly than the current sensory evidence.

In addition, we identified brain regions showing a parametric modulation of the BOLD signal depending on the

difficulty of the decision during the comparison period (difficulty regressor). We found that the BOLD signal in the ACC varied parametrically with the difficulty of the decision (see Figure 6 and Table 1).

DISCUSSION

We investigated how humans integrate current sensory evidence and prior average information during vibro-tactile decision making. First, we identified brain regions in which the BOLD response covaries parametrically with the deviation of the first vibration frequency from the average frequency during stimulus perception and maintenance indicating such an integration process. Second, we investigated in which of these brain regions changes in the BOLD signal additionally correlated with interindividual differences in the magnitude of the time-order effect, which reflects the degree to which perception and memory of the individual subject is biased by prior average information.

At the behavioral level, in line with previous psychophysical studies, we found an interaction between the magnitude of the first vibrotactile stimulus and the time order of presentation (Hellström, 1985; Helson, 1964). These
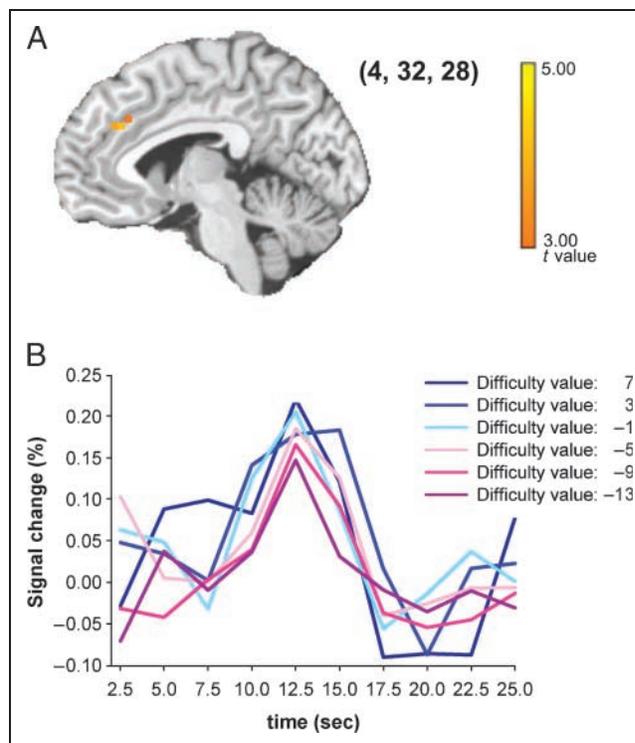

Figure 6. Neural correlates of decision difficulty. (A) The ACC is related to the difficulty of the decision, which is determined by the time-order effect, during the comparison period (shown at $p < .003$, uncorrected and projected on the MNI template "Colin."). (B) Corresponding time courses estimated from the activation cluster for the seven difficulty levels.

behavioral results suggest that prior average information did in fact bias vibrotactile decision making; that is, subjects formed an average representation and compared the second stimulus to a combination of this implicit average representation and the vibration frequency of the first stimulus.

During the encoding period, brain activity in S1, S2, thalamus, and ventral PMC covaried with the difference between the frequency of the first vibrotactile stimulus and the average frequency. These brain regions have previously been shown to contribute to vibrotactile attention and working memory (Burton, Sinclair, & McLaren, 2008; Kostopoulos et al., 2007; Li Hegner et al., 2007; Preuschhof et al., 2006; Luna et al., 2005; Romo et al., 2004; Romo & Salinas, 2003; Harris et al., 2001, 2002; Romo, Hernandez, Salinas, et al., 2002; Romo, Hernandez, Zainos, et al., 2002; Romo, Hernandez, Zainos, & Salinas, 1998). S1, S2, and the thalamus are part of the somatosensory processing stream; the ventral PMC is anatomically connected with the somatosensory cortices and contributes to attentional aspects of vibrotactile processing and encoding of vibrotactile stimuli (Preuschhof et al., 2006; Romo et al., 2004; Hagen, Zald, Thornton, & Pardo, 2002). The present data, however, go beyond these earlier findings in suggesting that these brain regions represent the part of the encoding network that integrates currently presented sensory evidence provided by the first vibrotactile stimulus and prior knowledge about the average frequency. There is ample evidence that early sensory brain regions have a more active role in cognitive processing than previously assumed (Pasternak & Greenlee, 2005; Ress & Heeger, 2003). Similarly, it has been shown that integration processes can occur at an early processing stage and in sensory brain regions including the thalamus (Kayser, Petkov, & Logothetis, 2008; Komura, Tamura, Uwano, Nishijo, & Ono, 2005; Fu et al., 2003; Schroeder et al., 2003; Foxe et al., 2000; Calvert et al., 1999). These studies, however, used tasks in which subjects have to integrate unimodal or cross-modal cues and stimuli. Beyond these findings, the present data show that early sensory brain regions already combine current sensory evidence with prior average information during stimulus encoding while the current vibration is still being presented and not only during the later judgment process (Basso & Wurtz, 1998; Carpenter & Williams, 1995). Moreover, the very same sensory brain regions that have previously been related to the encoding of vibrotactile frequencies in monkeys and in humans are involved in this integration process. The functional significance of this early incorporation of information about the prior stimulus distribution could be to supplement noisy sensory information to improve the fidelity of the memory trace for the upcoming maintenance and comparison period.

During the maintenance period, as opposed to the encoding period, brain activity in early somatosensory brain regions was not modulated by the deviation of the first vibration frequency from the average frequency. The only brain region showing such a modulation during the main-

tenance period was the IPS in the posterior parietal cortex (PPC). The PPC is a somatosensory association area containing cells responding to somatosensory stimulation (Breveglieri, Galletti, Gamberini, Passarelli, & Fattori, 2006; Kaas, 1993). Activation in the PPC has been associated with tactile object recognition (Stoeckel et al., 2004) and tactile attention (Burton et al., 1999; Pardo, Fox, & Raichle, 1991). In a previous fMRI study, we found that the PPC is associated with active maintenance and decision making during vibrotactile working memory in human subjects (Preuschhof et al., 2006). Our data suggest that the PPC is not only involved in the short-term maintenance of a vibrotactile stimulus and the integration of this recent sensory evidence for a specific stimulus (i.e., of the first vibration frequency) with current sensory evidence (i.e., the second vibration frequency). This region also contributes to the integration of recent sensory evidence and long-term representations about the average value of the stimulus set (i.e., the implicit average frequency).

The finding that activity in sensory brain regions is modulated by the difference between a current vibration frequency and the average frequency supports the view that prior information influences perceptual and mnemonic stimulus representations at a stage before the presentation of the second stimulus. The associated neural network seems to reflect processes involved in the specific integration of current sensory information by memory-based average information during the encoding and the delay period.

Neuronal adaptation of frequency selective neuronal populations (Krekelberg, Boynton, & van Wezel, 2006) could potentially contribute to the observed changes in BOLD signal. Human fMRI studies and rat single-unit recordings revealed evidence for adaptation for high-frequency vibrotactile stimulation (Li Hegner et al., 2007; Andermann, Ritt, Neimark, & Moore, 2004). Up to now there is, however, no evidence for frequency selective neuronal populations for the flutter frequency range. Also, neuronal adaptation should improve or impair performance in the vicinity of the adapting stimulus (i.e., close to the average frequency; Clifford et al., 2007; Kohn, 2007; Wark, Lundstrom, & Fairhall, 2007), but we did not observe changes in performance close to the average frequency. Instead we observed an interaction between the frequency of the first vibration and the time order of presentation. Thus, neither our behavioral data nor our fMRI data support the view that the results are due to neuronal adaptation.

However, if a brain region is involved in the integration of prior average information, its activity should not only reflect the integration process but should also correspond to the behavioral outcome. The BOLD signal in S2 during the encoding period and in the IPS during the maintenance period correlated with the individual magnitude of the time-order effect, providing strong evidence that these two regions are crucial for the integration of prior information at an early sensory level.

Our behavioral data show that the difficulty of the decision was determined by prior average information. Therefore, we also investigated in which brain regions the BOLD signal covaries with the difficulty of the discrimination during the comparison period. The only region showing such an effect was ACC. ACC has been associated with decision uncertainty and detection of conflicts (Yoshida & Ishii, 2006; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999). Supporting this view, the RT pattern revealed that in addition to lower accuracy, subjects showed increased RTs for decisions where the unpreferred (more difficult) time order had to be judged. This suggests that subjects did not just respond in relation to the average frequency, which would result in faster reactions for extreme values (further away from the average frequency) independent of the time order. Instead, subjects experienced increased uncertainty about their decision in trials with the unpreferred time order. This can be explained by the effect of the integration of average information into the representation of the current stimulus. For the unpreferred time order, this integration causes the representation of the first stimulus to drift toward the value of the second stimulus producing greater interference between the stimulus representations and increased uncertainty regarding which of the alternatives to choose. For the preferred time order, the representation of the first vibration drifts away from the value of the second vibration rendering the two stimulus representations more distinct and facilitating discrimination.

The vibrotactile delayed discrimination task has been intensively studied in humans (Kostopoulos et al., 2007; Li Hegner et al., 2007; Pleger et al., 2006; Preuschhof et al., 2006; Harris et al., 2002) and nonhuman primates (Romo & Salinas, 2003). Behavioral studies gave insight regarding the ability of humans and monkey to discriminate vibrotactile frequencies (Harris et al., 2001; Sinclair & Burton, 1996; Mountcastle, Steinmetz, & Romo, 1990). Single-unit recordings revealed the neural code necessary to perform the task (Lemus et al., 2007; Luna et al., 2005; Romo et al., 1999, 2003, 2004; Brody et al., 2003; Hernandez et al., 2000, 2002; Romo, Hernandez, Zainos, et al., 2002; Salinas et al., 2000). Computational models suggest how the working memory and the decision-making components of the task might be implemented on the level of neural networks (Deco, Scarano, & Soto-Faraco, 2007; Deco & Rolls, 2006; Machens, Romo, & Brody, 2005; Miller, Brody, Romo, & Wang, 2003). Collectively, computational studies, single-unit recordings, neuroimaging, and TMS studies elucidate the neurobiological mechanisms of vibrotactile perceptual decision making. These studies demonstrate that the integration of past sensory experience is a fundamental operation in perceptual decision making. The present study extends the understanding of vibrotactile decision making by showing that, in addition to short-term memory for a specific recent stimulus, long-term knowledge about the prior stimulus distribution plays a crucial role. An important question concerns the neural mechanism underlying the integration of prior information. Our data imply that information about the average vibration frequency is represented in the brain. This long-term representation of prior information might bias the neural activity in brain regions related to encoding (i.e., S2) and maintenance (i.e., PPC) of the current vibration frequency. During and after the presentation of a vibrotactile stimulus, these brain regions encode the difference between the current vibration frequency and the average frequency. Another possible mechanism is the Bayesian inference with probabilistic neuronal population codes (Ma, Beck, Latham, & Pouget, 2006; Stocker & Simoncelli, 2006; Knill & Pouget, 2004). According to this assumption, neuronal populations directly encode probability distributions regarding the value and the uncertainty for a sensory stimulus and also regarding prior knowledge about the stimulus distribution. Integration of current sensory evidence provided by the first vibration and prior knowledge about the average frequency would then be implemented by combining both probability distributions. Independent of the exact neural mechanism, the result of this integration process would be a sensory representation that is biased toward more probable or reliable stimuli. Regarding the interpretation of our data, this would mean that the uncertain representation of the current vibration frequency is combined with a more robust long-term representation of the implicit average information. As a result, the perception of the present frequency is biased toward the implicit average value. Importantly, with increasing delay length and therefore increasing uncertainty about the current vibration stimulus, the impact of prior information should increase and therefore enhance the time-order effect. This is exactly the behavioral pattern we found. The integration of prior information occurs in the same network of brain regions that has previously been related to the encoding and short-term maintenance of the vibration frequency and involves low-level somatosensory brain regions during stimulus perception but higher somatosensory association areas during stimulus maintenance.

Taken together, discrimination performance is based upon the difference between the neural representations of the stimuli to be compared. These representations do not only depend on the physical magnitude of the stimuli. Other important factors are previous experience and context information related to the sensory stimuli. The present data suggest that prior information about the mean of the stimulus set seems to play an important role. The finding that BOLD responses in brain regions related to somatosensory processing (S1, S2, thalamus, IFG, IPS) vary parametrically with the distance of the vibration frequency of the first stimulus from an assumed average stimulus indicates that prior information is already integrated into stimulus representations during an early phase of the decision-making process. Importantly, interindividual differences in the BOLD signal in S2 and the IPS reflect the degree to which individual subjects consider the prior average frequency relative to the current

vibration frequency. This finding strongly indicates that these two regions are crucially involved in the integration of priors and current sensory evidence. In more general terms, our data strongly support the notion that perception and subsequent decisions are biased toward typical, average, or prototype values. Like other authors before, Hellström (1985) reasoned that the purpose of the integration of prior average information is to support lost or noisy current information with stable average information. Although this use of context or prior probability information might lead to errors in some trials, it optimizes overall performance.

Acknowledgments

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