

Temporal dynamics of decisions on spatial categories and distances do not differ

Anna Oleksiak^{a,*}, Albert Postma^b, Ineke J.M. van der Ham^b, Richard J.A. van Wezel^a

^a *Helmholtz Research Institute, Functional Neurobiology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands*

^b *Helmholtz Research Institute, Experimental Psychology, Utrecht University, The Netherlands*

ARTICLE INFO

Article history:

Accepted 14 July 2008

Available online 5 September 2008

Keywords:

Speed-accuracy trade-off

Spatial relations

Coordinate and categorical representation

Temporal dynamics

ABSTRACT

It has been proposed that spatial relations can be encoded in two different ways: categorically, where the relative position of objects can be described in prepositional terms (to the left/right, above/below, etc.) and coordinately, where a precise distance between the objects is assessed. Processing of categorical and coordinate spatial relations is believed to rely on the parvo- and magnocellular pathways or small and large receptive fields, respectively. We employed the response signal speed-accuracy trade-off procedure to obtain a description of temporal dynamics of information transfer for categorical and coordinate spatial decisions. In the two tasks the same procedure and stimuli were used, while the instructions called for different types of discrimination. We found no differences in information accrual speed between the tasks as would be expected from the parvo/magno cells or small/large receptive fields distinction. Theoretical consequences of these findings are discussed.

© 2008 Elsevier Inc. All rights reserved.

1. Introduction

The brain instantly begins processing visual scenes when we open our eyes and the representations that we derive from incoming visual information can differ depending on our goals. For instance, in some situations it is enough to know that the bed stands to the left of the table. On the other hand, the assessment of distance separating two pieces of furniture might be more useful when one wants to pass between them. Thus, one representation would characterize relative spatial positions, while the other would involve exact distances. In the literature these two types of spatial representation are referred to as categorical and coordinate, respectively (Kosslyn, 1987; Kosslyn et al., 1989).

The main evidence supporting the idea that there is more than one way to encode spatial relations comes from studies on relative hemispheric differences in reaction times and/or accuracy between categorical and coordinate tasks. Categorical spatial decisions are reached faster and/or with fewer errors when the stimuli are presented in the right visual hemifield—the left hemisphere (LH) than in the left visual field—the right hemisphere (RH) (Kosslyn et al., 1989; Van der Ham, van Wezel, Oleksiak, & Postma, 2007). Likewise, decisions about coordinate spatial relations are faster and/or with higher accuracy when stimuli are shown to the RH than stimuli shown to the LH (Hellige & Michimata, 1989; Kosslyn et al., 1989; Michimata, 1997; Rybash & Hoyer, 1992). Still, a number of studies failed to find such interactions (Sergent, 1991; Wilkinson & Donnelly, 1999), especially for the categorical task and the LH advantage

(Hellige & Michimata, 1989; Van der Lubbe, Scholvinck, Kenemans, & Postma, 2006; see for a review Jager & Postma, 2003). Nevertheless, it is agreed that the reported hemispheric asymmetry is linked to the computational distinction between categorical and coordinate processes (Baker, Chabris, & Kosslyn, 1999).

Another line of evidence for two modes of encoding spatial relations comes from neural network simulations (Kosslyn, Chabris, Marsolek, & Koenig, 1992; Jacobs & Kosslyn, 1994; Baker et al., 1999). A neuronal network model that was trained to compute categorical and coordinate mappings performed better when hidden units were split into two subsystems: one with the input units carrying information to the categorical output units and the other set of input units contributing to the coordinate output units (Kosslyn et al., 1992).

Importantly, receptive field (RF) size was examined as a potential physiological factor that might underlie the proposed dissociation. It was suggested that larger, overlapping RFs might be more efficient in encoding precise spatial locations, the so called coarse coding mechanism (O'Reilly et al., 1990), which in turn might be relevant for coordinate judgments (Kosslyn et al., 1992). Accordingly, it was hypothesized that due to smaller, non-overlapping RFs space could be carved into distinct bins corresponding to spatial categories like for instance above/below or left/right (Kosslyn et al., 1992).

The finding that the computer network's performance in coordinate task was improved as RF size increased supported the first premise. Additionally, when the network was trained on the coordinate task, it spontaneously expanded the size of RFs, whereas training on the categorical task resulted in spontaneous development of small RFs (Kosslyn et al., 1992; Jacobs & Kosslyn, 1994; Baker et al., 1999).

* Corresponding author. Fax: +31 30 253 7730.

E-mail address: a.oleksiak@uu.nl (A. Oleksiak).

Kosslyn and co-workers (1992) as well as Roth and Hellige (1998) linked the hypothesized properties of the RFs contributing to the two spatial tasks to the well-studied classes of neurons: magno and parvo cells. In short, magno cells that contribute mainly to the magnocellular pathway have generally larger RFs, respond to higher temporal and lower spatial frequencies, display more rapid conduction of impulses and respond transiently and with shorter latencies (for a review see Merigan & Maunsell, 1993). On the other hand, parvo cells that contribute mainly to the parvocellular pathway have relatively smaller RFs, are more sensitive to lower temporal and higher spatial frequencies, their responses are sustained and display later response onsets.

Subsequently, Roth and Hellige (1998) and Hellige and Cumberland (2001) showed that a red background, which is known to disrupt processing relying on the magnocellular pathway (Livingstone & Hubel, 1984; de Monasterio & Schein, 1980; Breitmeyer & Williams, 1990), decreased performance in the coordinate task but not in the categorical task.

The suggestion that coordinate tasks might rely more on processing of the magnocellular pathway or simply larger RFs and categorical tasks more on the parvocellular pathway or smaller RFs seems feasible. However, some logical counterarguments can be raised. Namely, in general coordinate tasks require a somewhat higher spatial resolution of the representation to solve correctly the task and this intuitively would be more adequately accomplished by the means of smaller RFs of parvocellular neurons. In a similar line of reasoning one would rather expect an involvement of the magnocellular large RFs in computing rather crude positions in the categorical tasks. Moreover, in the vast majority of the studies the reported reaction times for coordinate tasks are longer than for categorical (e.g. Kosslyn et al., 1989; Michimata, 1997; Van der Ham et al., 2007; Van der Lubbe et al., 2006), which would counter the well known faster information transfer of the magnocellular system (e.g. Dreher, Fukada, & Rodieck, 1976; Schmolesky et al., 1998). Finally, in all divided-field presentation studies that investigated categorical and coordinate representations stimuli were presented parafoveally (at an eccentricity not larger than 3.5°), where visual input is predominantly received by parvocellular neurons (Azzopardi, Jones, & Cowey, 1999).

Considering just described discrepancies we set out to clarify whether the magno system or large RFs are indeed preferentially involved in processing categorical representations and whether the same is true for the interaction between coordinate tasks and parvo system or small RFs. We speculated, that the two tasks might differ in processing speed, since parvo- and magnocellular neurons differ in both, conduction velocity of their afferents (Dreher et al., 1976; Schiller & Malpeli, 1978; So & Shapley, 1979; Bullier & Henry, 1980; Vidyasagar, Kulikowski, Lipnicki, & Dreher, 2002) and in response latency (e.g. Munk, Nowak, Girard, Chounlamountri, & Bullier, 1995; Schmolesky et al., 1998; Maunsell et al., 1999). Alternatively, if there is no specific involvement of parvo and magno cells, Kosslyn and co-workers' model explicitly predicts that plainly the RF size plays a role in the categorical–coordinate spatial relations distinction. When we consider RFs sizes as a dissociating factor we still can expect to observe different speeds of information transfer in the two tasks due to the known negative correlation between RF size and response latency, i.e. the smaller RF the longer response delay (Weng, Yeh, Stoelzel, & Alonso, 2005).

The knowledge of temporal dynamics of information transfer in categorical and coordinate tasks will shed light on the question whether two distinct neuronal populations, corresponding to small and large RFs or parvo and magno pathways, are involved in these different spatial decisions. Such information can be obtained by the response signal speed-accuracy trade-off (SAT) procedure (Wickelgren, 1977), which allows an approximation of the minimal time necessary for performance

to depart from chance level. Furthermore, the SAT procedure estimates the speed at which performance reaches an asymptotic level, i.e. the information accrual rate.

Apart from the temporal description of the processes at stake, the SAT procedure has an advantage of controlling any possible speed-accuracy trade-offs. In a classical reaction time study most of the recorded data points lie in the vicinity of asymptotic performance. Since at low error rates variation in reaction times is large for extremely small changes in error percentage, speed-accuracy trade-off factor can exert a significant influence on results (Wickelgren, 1977). Moreover, a difference in response times between two conditions can be a consequence of differences in asymptotic accuracy, speed of processing or both (Reed, 1973; McElree & Doshier, 1989; Wickelgren, 1977). To control for such speed-accuracy trade-offs and to objectively compare the processing speed of cognitive tasks irrespective of differences in asymptotic performance we employed the above-mentioned SAT procedure that had been successfully implemented in other studies (e.g. Carrasco & McElree, 2001; Carrasco, McElree, Denisova, & Giordano, 2003; Carrasco, Giordano, & McElree, 2006; Doshier, Han, & Lu, 2004).

To recapitulate, on theoretical grounds we could expect differences in speed of information flow, represented in our study by the parameters estimates of the SAT function, between categorical and coordinate tasks. Owing to the contributions of magnocellular pathway or alternatively larger RFs the coordinate decisions are hypothesized to be processed faster compared to the categorical decisions that are believed to rely more on the parvocellular pathway or smaller RFs. However, it might be that we do not find any temporal dynamics differences implying that the mechanisms or neurons' features underlying the two types of spatial decisions are of some other sort than theorized by Kosslyn and others. It is also likely that we find a pattern of results where the categorical task is processed faster than the coordinate task, pointing to the aforementioned different spatial scale requirements for the two representations.

2. Methods

2.1. Subjects

Five subjects aged from 22 to 27 years old participated in our experiment. Four of the observers were unaware of the purposes of this study and one was an author (AO). All subjects had normal or corrected-to-normal vision. The naive subjects were paid for their participation.

2.2. Stimuli

The stimuli were presented on a standard color display (Sony CPD-E450, Sony Corporation, United States). The monitor resolution was set to 1280×1024 pixels with a refresh rate of 85 Hz. The responses and reaction times were recorded using the USB response pad (model RB 830 Cedrus®). Visual stimuli were generated with Presentation® 9.90 software (Neurobehavioral Systems).

With some adjustments, we used stimuli and instructions similar to those employed in the Van der Ham et al. (2007) study. The stimuli were composed of two black crosses displayed simultaneously on a light gray background, left and right of center, each subtending $2.6 \times 2.5^\circ$ of visual angle (Fig. 1). Each of the crosses had an accompanying dot subtending $.14 \times .13^\circ$ of visual angle, which could appear at one of three distances from the center of the cross in any of the four quadrants (Fig. 2). The crosses were aligned horizontally with the level of the fixation dot and their inner edges were placed 2.6° of visual angle away from the center.

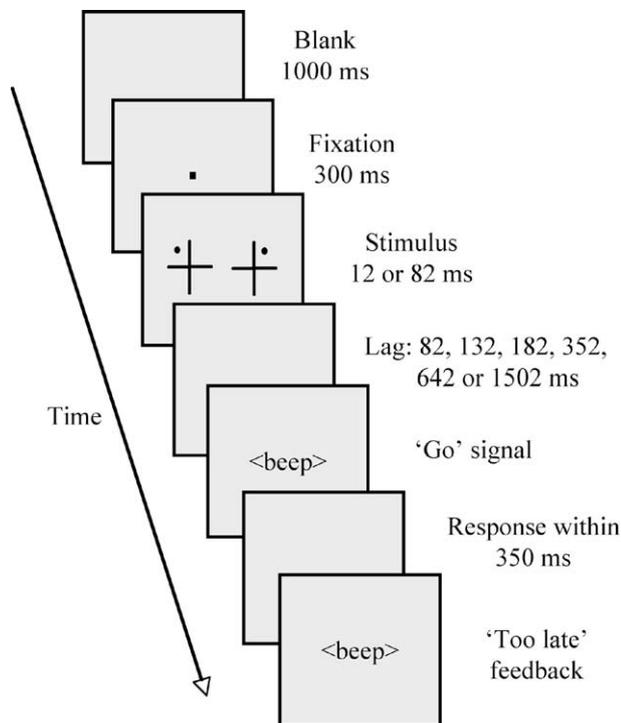


Fig. 1. The response signal speed-accuracy trade-off (SAT) procedure. Run of events within a single trial. The same stimuli and procedure were used for the two tasks, categorical and coordinate.

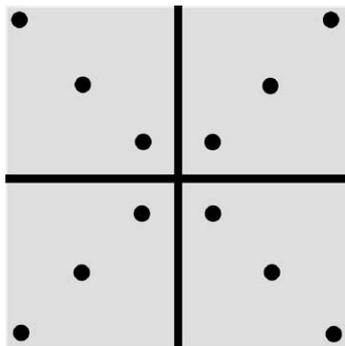


Fig. 2. Stimulus configuration. Each of the two crosses presented simultaneously was accompanied by a dot that could appear at one of 12 possible positions along the diagonals of the quadrants. The distance from the origin of the cross could be .39, 1.01 or 1.62° of visual angle.

2.3. Procedure

The subjects were seated 57 cm from the monitor inside a darkened room and a chin-rest prevented them from making significant head movements. The response pad was placed comfortably in front of the subjects. Responses were delivered by pressing one of two buttons with the index fingers. Our instruction stressed the importance of speed and accuracy in responding.

In our experimental design we took into account the possibility that the information accrual rate could differ depending on the amount of available visual information (Heller, Hertz, Kjaer, & Richmond, 1995). It has been shown that in neuronal responses most of the information is concentrated in the first one or two bursts of neuronal activity (Heller et al., 1995; Rolls, Tovee, & Panzeri, 1999; Tovee et al., 1993). The further accrual of new information has a shallower slope than the initial accumulation of visual

information (Heller et al., 1995). By introducing two stimulus durations we could investigate possible speed differences for both, initial (shorter exposure) and combined initial and later accumulation of visual information (longer exposure). If there were any temporal dynamics dissimilarities between categorical and coordinate spatial relations processes, these could be evident in the first (fast), second (slower) or both information accrual phases. Brief stimulus exposure was constrained by the maximum refresh rate of the monitor (85 Hz); as a result one frame lasted 12 ms. On the other hand, longer exposure was mitigated by the timing of the response signals, which had to be identical for the two display conditions. That is, an exposure longer than 82 ms would eliminate the shortest response lags from the paradigm. In addition, longer stimulus presentations would allow eye movements that might confound results.

An overview of the response signal SAT procedure we used is depicted in Fig. 1. At the beginning of each trial subjects stared at a blank, light gray screen for 1000 ms. Once the time had elapsed, a fixation dot appeared in the center of the screen for 300 ms. This was followed by presentation of the two crosses, each with an associated dot that would last either 12 or 82 ms. When the stimuli disappeared the blank screen returned for 82, 132, 182, 352, 642 or 1502 ms. At the end of a lag a 500 Hz tone was sounded indicating to the subjects the need to deliver a response. Participants were given 350 ms to press one of the two buttons; otherwise a 1000 Hz tone announced that the response was “too late”. Because of the six lags we used, the range of obtained response times enabled us to sample the full time course of processes involved in the task. This began during the very early stages characterized by chance level performance and ended with the late stage of decision-making where additional time failed to improve performance.

All of the observers performed two to four practice sessions 22 min each. The four main 50-min sessions were completed within 2–8 days. During two of the sessions observers were instructed to indicate whether the dots appeared in corresponding or different quadrants of the two crosses—categorical task. This task required only categorical spatial information since a precise position of the dots was irrelevant. The other two sessions necessitated an assessment of distances between the dots and the origins of the crosses. The task was to decide whether those distances varied irrespective of the quadrant in which the dots were shown—coordinate task. The set of stimuli used for both instructions was exactly the same while the order of the instructions was counter-balanced across subjects. The varying lags (6) and stimulus exposures (2) were randomized across trials within each session. On average subjects completed 2370 valid trials per instruction (min 2048—max 2521). With respect to other lags, we doubled the number of trials with the two shortest lags (82 and 132 ms), because under those conditions observed responses most often fell outside the allotted time window.

2.4. Data analysis

From the responses collected, we calculated discriminability (d'), which gave us a bias-free measure of performance at each interruption point (corresponding to the six lags). The z-transforms of the fraction correct for match and non-match trials yielded the d' values ($d' = z_{\text{same}} + z_{\text{different}}$). In order to avoid infinite z-values due to a limited number of observations n , probability of 1 was clipped at $1 - 1/n$ (Wickens, 2002). We plotted discriminability (d') as a function of average total processing time, corresponding to the time between stimulus onset and response. Data points (within and across subjects) were fit with an exponential approach to a limit represented by the SAT function:

$$d'(t) = \lambda[1 - e^{-\beta(t-\delta)}], \quad \text{for } t > \delta, \text{ else } 0, \quad (1)$$

In Eq. (1) the estimate of the asymptotic accuracy is represented by λ while the temporal dynamics parameters of information accrual and intercept appear as β and δ , respectively (Doshier, 1979; Reed, 1973; Wickelgren, 1977). Specifically, the λ reflects discriminability at unlimited processing time. Parameter β stands for the rate at which discriminability rises from chance level ($d' = 0$) to asymptote. Parameter δ refers to an intercept that describes the point in time when performance begins to depart from chance. Taken β and δ one can calculate a composite value by summing the estimates of intercept and reciprocal of the accrual rate ($\delta + 1/\beta$).

We performed global nonlinear curve fitting using GraphPad Prism version 4.0c for Mac OS X (GraphPad Software, San Diego California USA). With the intent of testing how the three parameters were influenced by the instructions (categorical vs. coordinate task), we examined models that spanned from null, which assigned a single set of parameters to the two sets of data ($1\lambda 1\beta 1\delta$), to a full model comprised of unique parameters for each data set ($2\lambda 2\beta 2\delta$), with all other possibilities in between ($2\lambda 1\beta 1\delta$, $1\lambda 2\beta 1\delta$, $1\lambda 1\beta 2\delta$, $2\lambda 2\beta 1\delta$, $2\lambda 1\beta 2\delta$, $1\lambda 2\beta 2\delta$). The quality of the fits was determined by the adjusted R^2 statistics, which indicated the proportion of variance explained by the model corrected for the number of free parameters. The statistical significance of the compared nested models was achieved by performing an F test and further deriving a p -value using a standard table (Motulsky & Ransnas, 1987). The following equation was used to calculate F -values:

$$F = \frac{(SS_1 - SS_2)/(df_1 - df_2)}{SS_2/df_2} \quad (2)$$

Here SS corresponds to the sum of squares due to error, df to the degrees of freedom (number of data points minus number of free parameters) and the subscript 1 to the model with fewer parameters. The F statistics, repeated measures ANOVA (Trujilli-Ortiz et al., 2004) were carried out in MATLAB.

3. Results

3.1. Performance

By interrupting the decision process at six points in time we were able to probe the temporal dynamics of formed spatial representations. We examined response time as a function of discriminability (bias-free accuracy measure—see Section 2) thereby, controlling for possible speed-accuracy trade-offs.

Overall, each subject performed better when the stimulus duration was longer (average across lags and participants: 74% vs. 77% for the quadrant task and 61% vs. 65% correct for the distance task for 12 and 82 ms, respectively). A two-way repeated measures ANOVA performed on d' values (an average of six response lags) showed significant effects of instruction ($F(1,4) = 40.42$, $p = .00007$; mean d' values for the categorical and coordinate task were 2.15 and .84, respectively) and stimulus duration ($F(1,4) = 3.99$, $p = 0.0208$; mean d' value for the 12 ms exposure was 1.31 and for the 82 ms presentation 1.68) that did not interact ($F(1,4) = .05$, $p = 0.82$). Similarly, when only the last response lag reflective of performance at the maximum processing time was considered, a repeated measures two-way ANOVA revealed a task effect ($F(1,4) = 171.82$, $p = .0002$; mean d' value 3.77 for the categorical and 1.5 for the coordinate task) and an exposure effect ($F(1,4) = 15.17$, $p = .018$) with a higher discriminability for 82 ms exposure duration (3.05 d' units) than for 12 ms (2.22 d' units), whereas the interaction of these factors was not significant ($F(1,4) = 1.20$, $p = 0.33$). Since the interaction between the task and presentation duration was not significant and, more importantly, because our main goal was to compare the temporal

dynamics of categorical and coordinate spatial representations, in further hierarchical model-testing procedure we will consider the two stimulus exposure durations separately and thereby investigate only the influence of instruction (categorical vs. coordinate) on the three parameters of Eq. (1).

3.2. Curve fitting

The procedure of global model fitting was carried out independently for the two stimulus durations and the hierarchical model-testing procedure yielded qualitatively the same best fitting models for all observers and for the average data for both exposure conditions. The graph in Fig. 3A illustrates the average data for the brief exposure (12 ms) condition with the circles representing an average discriminability (in d' units) at the average processing time of each response signal lag (in seconds). The data sets are split into two tasks—categorical (filled circles) and coordinate (open circles). The best fitting models are described in Fig. 3A by the solid line for the categorical, and the dashed line for the coordinate task. The same conventions are used in the Fig. 3B that depicts the average results for the longer stimulus presentation (82 ms) condition. These models resulted from the evaluation of fits of nested models that systematically varied the three parameters of Eq. (1) with the instruction as a factor.

We will begin by considering the models for the brief stimulus presentation. It is apparent from Fig. 3A that the categorical and coordinate instructions resulted in different levels of asymptotic performance, that is the lambda parameter of the SAT function. Accordingly, for all five subjects, the best fitting models assigned separate asymptote parameters (λ) to categorical and coordinate instructions (for parameter estimates of the best models for individual observers and for the average data see Table 1). More importantly, the processing speed parameters β (accrual rate) and δ (intercept) reflected no significant differences between the two tasks since the best fitting global model allocated common β and δ to the categorical and coordinate tasks (Table 1). As a result, the global model that produced the best fit corrected for the number of free parameters was a model with distinct lambda's (asymptote's) for the categorical and coordinate tasks and a common β (accrual rate) and δ (time of departure from a chance performance) parameters with an adjusted R^2 value of .985 for the average data (more details in Table 1). The models that contained a shared asymptote resulted in smaller adjusted R^2 values for individual as well as for the average data ($1\lambda 1\beta 1\delta$ —null model, $adjR^2 = .182$; $1\lambda 2\beta 2\delta$, $adjR^2 = .942$; $1\lambda 1\beta 2\delta$, $adjR^2 = .214$ and $1\lambda 2\beta 1\delta$, $adjR^2 = .827$). Correspondingly, when two discrete accrual rates (β) were assigned to the two data sets ($2\lambda 2\beta 2\delta$, $adjR^2 = .989$) or two separate intercepts (δ) ($2\lambda 1\beta 2\delta$, $adjR^2 = .983$) or both unique β and δ ($2\lambda 2\beta 2\delta$ —full model, $adjR^2 = .985$ for categorical data and $adjR^2 = .970$ for coordinate data) the adjusted R^2 values were either not improved or an additional parameter did not significantly decrease residual errors according to the results of Eq. (2) (for more detail about the full models' fits refer to Table 2). We chose the more parsimonious $2\lambda 1\beta 1\delta$ model and conclude that instruction only affects the asymptotic performance and not the speed parameters.

Using longer stimulus durations we could additionally sample the temporal dynamics of a later stage of visual information accumulation (Heller et al., 1995). The best fitting models for the longer exposure again consistently distinguished separate asymptotes (λ) for the two tasks for all subjects and for the averaged data (Fig. 3B and Table 1). Comparable to the brief presentations, the rate of information accrual (β) and the intercept (δ) were not significantly different between the instructions thereby for all the subjects the best model allotted common β and δ ($adjR^2 = .974$ for the average data; Fig. 3B and Table 1). The models with one λ parameter for the two instructions produced poor description of the individual and the

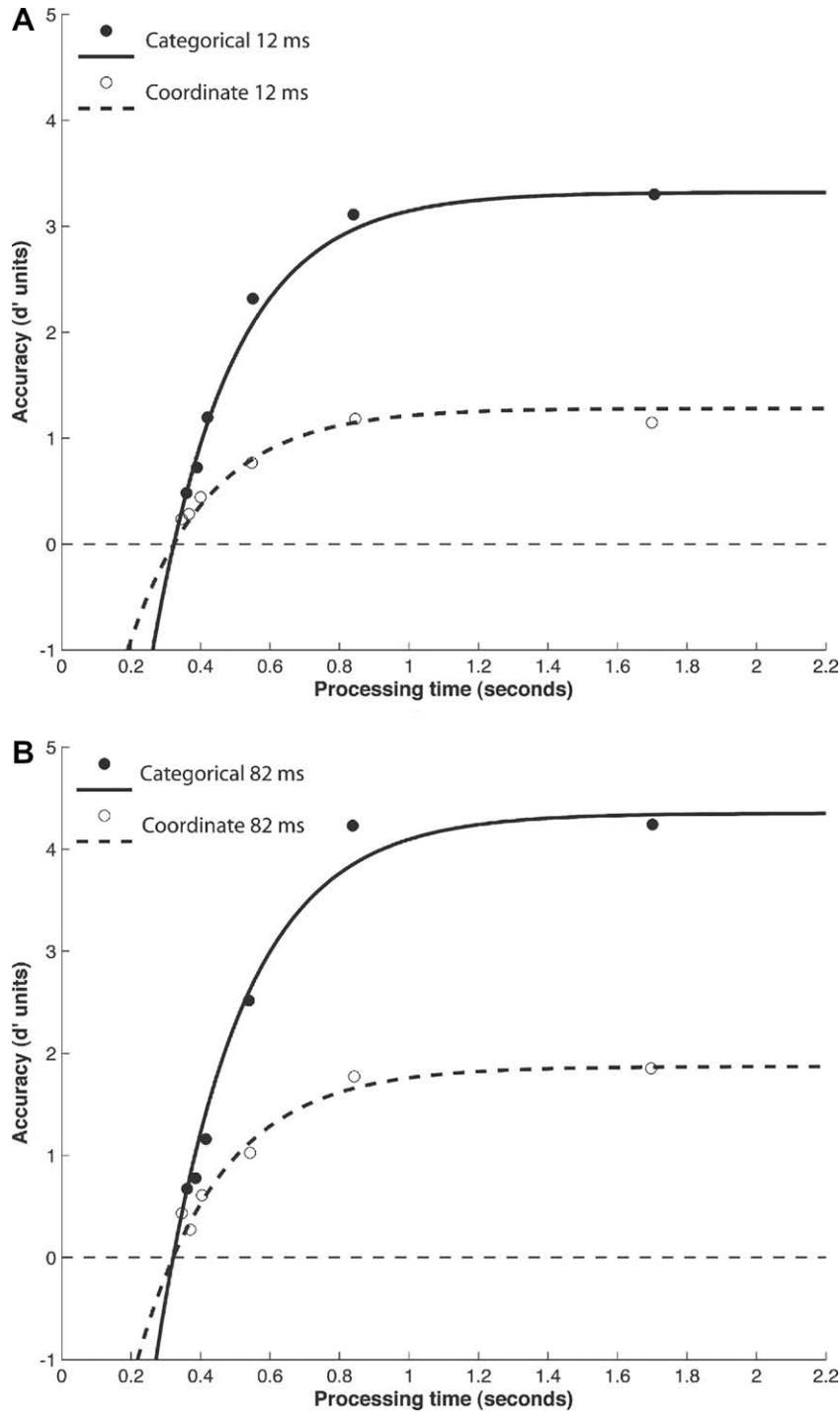


Fig. 3. (A) Average results ($n = 5$) of the response signal SAT procedure for the brief (12 ms) stimulus display. Average discrimination accuracy (in d' units) is plotted as a function of processing time (in seconds) in categorical (filled circles) and coordinate (empty circles). The smooth lines represent the best fitting models ($2\lambda 1\beta 1\delta$) with separate asymptotes but same accrual rate and intercept for categorical (solid) and coordinate (dashed) tasks. (B) Average results ($n = 5$) of the response signal SAT procedure for the longer (82 ms) stimulus display. The conventions are the same as in A.

average data ($1\lambda 1\beta 1\delta$, $_{adj}R^2 = .536$; $1\lambda 2\beta 2\delta$, $_{adj}R^2 = .936$; $1\lambda 1\beta 2\delta$, $_{adj}R^2 = .519$ and $1\lambda 2\beta 1\delta$, $_{adj}R^2 = .886$). On the other hand, fuller models with separate β and/or δ did not result in better fits or did not significantly reduce residual errors when compared to the $2\lambda 1\beta 1\delta$ model with the use of Eq. (2) ($2\lambda 2\beta 1\delta$, $_{adj}R^2 = .972$; $2\lambda 1\beta 2\delta$, $_{adj}R^2 = .975$; $2\lambda 2\beta 2\delta$, $_{adj}R^2 = .968$ for categorical data and $_{adj}R^2 = .943$ for coordinate data; see Table 2 for details of the full models).

Our results clearly demonstrate that instruction (categorical vs. coordinate task) significantly influences asymptotic performance for all observers. This was reflected in separate λ parameter esti-

mates of Eq. (1) for the two instructions as rendering the best fitting global models. The processing speed (β and δ parameter estimates), however, did not differ between the distance and quadrant tasks; hence, more parsimonious global models (with common processing speed parameters) were assigned. Moreover, the same best global model ($2\lambda 1\beta 1\delta$) was assigned for both stimulus duration conditions. This strongly suggests that the processes underlying categorical and coordinate spatial representations have similar temporal dynamics in both early and later stages of information transfer.

Table 1
Exponential descriptive parameters' estimates for the best fitting models ($2\lambda 1\beta 1\delta$) for the categorical and coordinate tasks presented in Fig. 3

Parameter	Observer					Mean
	AO	BD	MB	NM	SK	
Exposure 12 ms						
<i>Discriminability λ (in d' units)</i>						
Categorical	4.10	2.20	4.0	3.94	2.65	3.32
Coordinate	1.53	.57	1.30	1.44	1.30	1.28
<i>Common processing speed (in ms)</i>						
Rate $1/\beta$	110	318	215	300	169	230
Intercept δ	345	302	339	334	329	323
Composite value $\delta + 1/\beta$	455	620	554	634	498	553
Adjusted R^2	.934	.899	.982	.983	.975	.985
Exposure 82 ms						
<i>Discriminability λ (in d' units)</i>						
Categorical	4.44	4.28	4.61	4.74	4.16	4.35
Coordinate	1.6	1.73	2.08	2.24	1.99	1.87
<i>Common processing speed (in ms)</i>						
Rate $1/\beta$	124	302	259	254	246	239
Intercept δ	334	325	336	352	227	321
Composite value $\delta + 1/\beta$	458	627	595	606	573	560
Adjusted R^2	.956	.908	.957	.977	.984	.974

Table 2
Exponential descriptive parameters' estimates for the full model ($2\lambda 2\beta 2\delta$) for the categorical and coordinate tasks

Parameter	Observer					Mean
	AO	BD	MB	NM	SK	
Exposure 12 ms						
<i>Discriminability λ (in d' units)</i>						
Categorical	4.16	2.36	3.97	3.93	2.62	3.37
Coordinate	1.36	.50	1.42	1.43	1.40	1.25
<i>Rate β (in ms)</i>						
Categorical	349	437	206	290	154	227
Coordinate	326	75	313	340	261	238
<i>Intercept δ (in ms)</i>						
Categorical	113	277	340	340	334	326
Coordinate	64	327	334	297	307	301
<i>Composite value $\delta + 1/\beta$ (in ms)</i>						
Categorical	462	714	546	630	488	553
Coordinate	390	402	647	636	568	539
<i>Adjusted R^2</i>						
Categorical	.932	.930	.970	.995	.958	.985
Coordinate	.898	.625	.975	.825	.955	.970
Exposure 82 ms						
<i>Discriminability λ (in d' units)</i>						
Categorical	4.49	4.21	4.64	4.72	4.16	4.33
Coordinate	1.46	1.81	2.04	2.28	1.99	1.90
<i>Rate β (in ms)</i>						
Categorical	129	260	271	246	244	215
Coordinate	92	429	226	296	249	305
<i>Intercept δ (in ms)</i>						
Categorical	336	343	333	356	328	329
Coordinate	313	249	348	331	323	290
<i>Composite value $\delta + 1/\beta$ (in ms)</i>						
Categorical	465	603	604	602	572	544
Coordinate	404	678	574	627	572	595
<i>Adjusted R^2</i>						
Categorical	.973	.908	.957	.973	.990	.968
Coordinate	.465	.878	.866	.948	.922	.943

4. Discussion

Here, we investigated temporal dynamics of two cognitive processes. By changing only the instruction and using the same stimuli we were able to directly compare the time courses of two types of spatial relations encoding: distance assessment in 2D (coordinate

task) and spatial categorization (categorical task). Although, the same stimulus display was used in the two tasks, observers had to extract (partially) different visual information that served different goals. We varied stimulus duration (12 and 82 ms), since differences in dynamics could occur at the very early stage of information accrual, when all the incoming information is new,

or at a later stage, when only a fraction of the transferred information is new (Heller et al., 1995).

In order to assess the temporal dynamics of decisions based on either the categorical or coordinate aspect of visual information we employed the response signal SAT procedure (Wickelgren, 1977). This method allowed us to estimate an intercept (δ from Eq. (1)) that corresponds to a minimum time necessary for performance to depart from a chance level, and an accrual rate (β from Eq. (1)) that gives an indication of with what speed performance reaches an asymptotic level. In addition, this method controls for any speed-accuracy trade-offs and permits a comparison of speed of processing irrespective of task related differences in asymptotic performance.

Since categorical and coordinate spatial relations processes are thought to rely on the parvo- and magnocellular pathways, respectively, or alternatively on the input from correspondingly small and large RFs, we anticipated differences in the temporal dynamics of decisions. We hypothesized that the difference in neuronal response latency that was reported for magno- and parvocellular pathways (Munk et al., 1995; Schmolesky et al., 1998; Maunsell et al., 1999) or alternatively, for larger and smaller RFs (Weng et al., 2005), might be reflected in a smaller δ parameter in the coordinate compared to the categorical task. In a similar fashion, since afferents of the magnocellular pathway were found to have higher signal conduction velocity than those of the parvocellular system (Dreher et al., 1976; Schiller & Malpeli, 1978; So & Shapley, 1979; Bullier & Henry, 1980; Vidyasagar et al., 2002), we expected to obtain higher estimates of β parameter for the coordinate than for the categorical instruction.

In case of a classical response time paradigm any variation in reaction times can be attributed to the speed of processing or alternatively, to the level of difficulty of the tasks, and the most likely a mixture of both. Given that in most of the studies on coordinate and categorical spatial processing (e.g. Van der Lubbe et al., 2006; Van der Ham et al., 2007), including the current one, the coordinate task is more difficult (higher error rates) than the categorical, a simple measure of reaction time cannot unambiguously demonstrate processing speed differences. The response signal SAT procedure we implemented here offered a good solution to this problem.

Our results show no differences in speed of processing between the categorical and coordinate tasks. Neither for the brief stimulus display (12 ms) nor for the longer one (82 ms) did the best fitting model contain different speed parameters for the two instructions. The assigned common β and δ parameters were coupled with two separate asymptote parameters with a higher d' value for the categorical data set than for the coordinate.

There might be a number of reasons why we demonstrated very similar speed of processing for the categorical and coordinate representations. First of all, one might suggest that the tasks we used did not tap the hypothesized spatial representations. However, the stimulus we employed, a cross with an accompanying dot, was used before with success (Van der Ham et al., 2007). In particular, with such a stimulus Van der Ham and co-workers (2007) demonstrated the visual field and task interaction proposed by Kosslyn et al. (1989).

It might be argued that sensitivity of the response signal SAT method is too crude to detect hypothesized temporal differences. However, in studies by Carrasco and associates (2003, 2006) the same method proved to be sensitive enough to detect dissociation in processing speed for two eccentricities. Moreover, the authors attributed the smaller δ parameter (a difference of 87 ms) for larger eccentricity (9° vs. 4° of visual angle) to the involvement of magno cells (Carrasco et al., 2003, 2006), since they are more abundant in the periphery of the visual field than in the fovea (Azzopardi et al., 1999).

Inevitably, our current results need to be considered in the light of the studies by Roth and Hellige (1998), Hellige and Cumberland (2001) and Okubo and Michimata (2002, 2004) that tested a relation of categorical and coordinate representations with some purported properties of magno- and parvocellular pathways. Particularly, Roth and Hellige (1998) and Hellige and Cumberland (2001) attenuated the processing of the magnocellular pathway by presenting stimuli on a red background and looked at how this manipulation influenced performance in categorical and coordinate tasks. They based their prediction on the Kosslyn's premise and expected that the red background (known to disrupt the transient M channel; Bretmeier & Williams, 1990) would only affect the coordinate task, since it should rely more on magno cells than the categorical task. In the first study Roth and Hellige (1998) analysed only response times, because the percentage of error was very low (less than 5%). Even though the researchers found a large increase in reaction time for the coordinate task when presented on the red screen, the fact that there was a ceiling effect in error rate dictates some caution in drawing strong conclusions. The follow up study (Hellige & Cumberland, 2001) supports this concern since performance in coordinate task was decreased (by ~8.5%—estimated from their Fig. 1) in the red background condition, but at the same time reaction times did not show an interaction between task and background color with an increase in the coordinate task by only 16 ms.

Okubo and Michimata (2002, 2004), on the other hand, manipulated spatial frequency content of stimuli and observed performance for categorical and coordinate instructions. This design was inspired by the notion that large RFs process low spatial frequencies, while small RFs are more suitable for higher spatial frequencies. When they presented contrast-balanced dots that allegedly were devoid of low spatial frequencies, an interaction of visual field and instruction predicted by Kosslyn disappeared (Okubo & Michimata, 2002). From this reaction time effect they concluded that coordinate spatial relations rely on low spatial frequencies that are predominantly processed by the right hemisphere. However, there was a strong main effect of stimulus type (slower responses to the contrast-balanced stimuli) meaning that actually both tasks were negatively affected by removing low spatial frequencies. Unfortunately, the authors did not report anything about an interaction of task and stimulus type (with or without low spatial frequencies) but from mean response times it is obvious that response latencies were 61 ms longer for the contrast-balanced stimuli in the categorical task, whereas in the coordinate instruction this increase was smaller (41 ms). Moreover, the error rates were not analysed due to a very small percentage of errors.

In a similar line of thinking, they designed stimuli that were devoid of high spatial frequencies and looked at the performance in the two spatial tasks (Okubo & Michimata, 2004). This time the errors of 3.78% and 7.04% (for categorical and coordinate task, respectively) seemed to the authors large enough to analyse. Importantly, they show a significant interaction of stimulus type and instruction, where performance in categorical task was worse for low-pass-filtered stimuli, but strangely the coordinate task was improved in this condition. Although, the decrease in performance for the categorical task for low-pass-filtered stimuli was predicted by the Kosslyn's theory, the improvement in the coordinate task is difficult to explain. Finally, it is hard to interpret the results unambiguously, due to a lack of interaction between task and stimulus type for response times.

These four studies that have a direct connection to our results, but also other experiments within this research field, seem to have one main drawback that bars unequivocal conclusions. Performance level in these studies is at a ceiling level and at the same time, response time differences between main conditions are not very large. Still, exactly at this high performance level the variation

in response latencies is enormous for very small differences in errors (Wickelgren, 1977). Consequently, this variability is very large compared to most response time differences, which makes speed-accuracy trade-offs a significant factor. By using the response signal speed-accuracy trade-off procedure we minimized such confounds.

On theoretical grounds the current results indicate that the magno and parvo pathways or equivalently, large and small RFs play a less important role in forming the categorical and coordinate spatial representations than suggested by Kosslyn's proposal and some preceding reports. One cannot exclude that previously found double dissociation of categorical and coordinate representation to the left and right hemisphere correspondingly reflected not a differential contribution of magno and parvo cells in the two hemispheres, but asymmetries related to the difficulty of the processed task. Such explanation was already put forward in a number of studies (Parrot, Doyon, Demonet, & Cardebat, 1999; Sergent, 1991; Slotnick, Moo, Tesoro, & Hart, 2001), however, only recently this issue was specifically addressed in an imaging experiment. In particular, Martin and associates (2008) suggested a hypothesis that these two types of spatial relations belong to the same processing continuum and that the previously reported hemispheric specialization surfaced as a consequence of differing complexity of the same basic representation. This premise was supported by their results where categorical and coordinate tasks evoked strong BOLD signal in a similar fronto-parieto-occipital network. Importantly, some parts of this common network (mostly attention related) lit up parametrically and asymmetrically with an increasing difficulty of the task.

We might also consider our results in the light of neurophysiological findings. Our distance task resulted in a much lower discriminability than the quadrant task, although the temporal dynamics of the two did not differ significantly. It is therefore more likely that these two spatial representations rely on the same neuronal population and differ mainly in the amount of visual evidence necessary to reach a decent level of performance. This would be in turn understood as a coarse-to-fine mode of visual processing with categorical representation corresponding to the coarse phase of information coding and coordinate relating to the later-stage fine representation. Significantly, such dynamic changes of spatial resolution of visual information were observed within a single neuron which receptive field shrank with elapsed time—note a negative correlation between RF size and spatial resolution (Allen & Freeman, 2006; Rukhsenas, Bulatov, & Heggelund, 2007; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006). Such analogy seems adequate if we consider the intuitive notion that a more detailed coordinate representation is preceded by a categorical, coarse grasp of a visual scene.

References

- Allen, E. A., & Freeman, R. D. (2006). Dynamic spatial processing originates in early visual pathways. *Journal of Neuroscience*, 26, 11763–11774.
- Azzopardi, P., Jones, K. E., & Cowey, A. (1999). Uneven mapping of magnocellular and parvocellular projections from the lateral geniculate nucleus to the striate cortex in the macaque monkey. *Vision Research*, 39, 2179–2189.
- Baker, D. P., Chabris, C. F., & Kosslyn, S. M. (1999). Encoding categorical and coordinate spatial relations without input-output correlations: New simulation models. *Cognitive Science*, 23, 33–51.
- Breitmeyer, B. G., & Williams, M. C. (1990). Effects of isoluminant-background color on metacontrast and stroboscopic motion: Interactions between sustained (P) and transient (M) channels. *Vision Research*, 30, 1069–1075.
- Bullier, J., & Henry, G. H. (1980). Ordinal position and afferent input of neurons in monkey striate cortex. *Journal of Computational Neurology*, 193, 913–935.
- Carrasco, M., Giordano, A. M., & McElree, B. (2006). Attention speeds processing across eccentricity: Feature and conjunction searches. *Vision Research*, 46, 2028–2040.
- Carrasco, M., & McElree, B. (2001). Covert attention accelerates the rate of visual information processing. *Proceedings of the National Academy of Science USA*, 98, 5363–5367.
- Carrasco, M., McElree, B., Denisova, K., & Giordano, A. M. (2003). Speed of visual processing increases with eccentricity. *Nature Neuroscience*, 6, 699–700.
- de Monasterio, F. M., & Schein, S. J. (1980). Protan-like spectral sensitivity of foveal Y ganglion cells of the retina of macaque monkeys. *Journal of Physiology*, 299, 385–396.
- Doshier, B. A. (1979). Empirical approaches to information processing: Speed-accuracy tradeoff functions or reaction time—A reply. *Acta Psychologica (Amsterdam)*, 43, 347–359.
- Doshier, B. A., Han, S., & Lu, Z. L. (2004). Parallel processing in visual search asymmetry. *Journal of Experimental Psychology: Human Perception & Performance*, 30, 3–27.
- Dreher, B., Fukada, Y., & Rodieck, R. W. (1976). Identification, classification and anatomical segregation of cells with X-like and Y-like properties in the lateral geniculate nucleus of old-world primates. *Journal of Physiology*, 258, 433–452.
- Heller, J., Hertz, J. A., Kjaer, T. W., & Richmond, B. J. (1995). Information flow and temporal coding in primate pattern vision. *Journal of Computational Neuroscience*, 2, 175–193.
- Hellige, J. B., & Cumberland, N. (2001). Categorical and coordinate spatial processing: More on contributions of the transient/magnocellular visual system. *Brain & Cognition*, 45, 155–163.
- Hellige, J. B., & Michimata, C. (1989). Categorization versus distance: Hemispheric differences for processing spatial information. *Memory & Cognition*, 17, 770–776.
- Jacobs, R. A., & Kosslyn, S. M. (1994). Encoding shape and spatial relations: The role of receptive field size in coordinating complementary representations. *Cognitive Science*, 18, 367–386.
- Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: A review of the current evidence. *Neuropsychologia*, 41, 504–515.
- Kosslyn, S. M. (1987). Seeing and imagining in the cerebral hemispheres: A computational approach. *Psychological Review*, 94, 148–175.
- Kosslyn, S. M., Chabris, C. F., Marsolek, C. J., & Koenig, O. (1992). Categorical versus coordinate spatial relations: Computational analyses and computer simulations. *Journal of Experimental Psychology: Human Perception & Performance*, 18, 562–577.
- Kosslyn, S. M., Koenig, O., Barrett, A., Cave, C. B., Tang, J., & Gabrieli, J. D. (1989). Evidence for two types of spatial representations: Hemispheric specialization for categorical and coordinate relations. *Journal of Experimental Psychology: Human Perception & Performance*, 15, 723–735.
- Livingstone, M. S., & Hubel, D. H. (1984). Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience*, 4, 309–356.
- Martin, R., Houssemand, C., Schiltz, C., Burnod, Y., & Alexandre, F. (2008). Is there continuity between categorical and coordinate spatial relations coding? Evidence from a grid/no-grid working memory paradigm. *Neuropsychologia*, 46, 576–594.
- Maunsell, J. H., Ghose, G. M., Assad, J. A., McAdams, C. J., Boudreau, C. E., & Noerager, B. D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience*, 16, 1–14.
- McElree, B., & Doshier, B. A. (1989). Serial position and set size in short term memory: The time course of memory. *Journal of Experimental Psychology: General*, 118, 346–373.
- Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, 16, 369–402.
- Michimata, C. (1997). Hemispheric processing of categorical and coordinate spatial relations in vision and visual imagery. *Brain & Cognition*, 33, 370–387.
- Motulsky, H. J., & Ransnas, L. A. (1987). Fitting curves to data using nonlinear regression: A practical and nonmathematical review. *Journal of the Federation of American Societies for Experimental Biology*, 1, 365–374.
- Munk, M. H., Nowak, L. G., Girard, P., Choumlamountri, N., & Bullier, J. (1995). Visual latencies in cytochrome oxidase bands of macaque area V2. *Proceedings of the National Academy of Science USA*, 92, 988–992.
- Okubo, M., & Michimata, C. (2002). Hemispheric processing of categorical and coordinate spatial relations in the absence of low spatial frequencies. *Journal of Cognitive Neuroscience*, 14, 291–297.
- Okubo, M., & Michimata, C. (2004). The role of high spatial frequencies in hemispheric processing of categorical and coordinate spatial relations. *Journal of Cognitive Neuroscience*, 16, 1576–1582.
- O'Reilly, R. C., Kosslyn, S. M., Marsolek, C. J., & Chabris, C. F. (1990). Receptive field characteristics that allow parietal lobe neurons to encode spatial properties of visual input: A computational analysis. *Journal of Cognitive Neuroscience*, 2, 141–155.
- Parrot, M., Doyon, B., Demonet, J. F., & Cardebat, D. (1999). Hemispheric preponderance in categorical and coordinate visual processes. *Neuropsychologia*, 37, 1215–1225.
- Reed, A. (1973). Speed-accuracy trade-off in recognition memory. *Science*, 181, 574–576.
- Rolls, E. T., Tovee, M. J., & Panzeri, S. (1999). The neurophysiology of backward visual masking: Information analysis. *Journal of Cognitive Neuroscience*, 11, 300–311.
- Roth, E. C., & Hellige, J. B. (1998). Spatial processing and hemispheric asymmetry. Contributions of the transient/magnocellular visual system. *Journal of Cognitive Neuroscience*, 10, 472–484.
- Rukhsenas, O., Bulatov, A., & Heggelund, P. (2007). Dynamics of spatial resolution of single units in the lateral geniculate nucleus of cat during brief visual stimulation. *Journal of Neurophysiology*, 97, 1445–1456.
- Rybash, J. M., & Hoyer, W. J. (1992). Hemispheric specialization for categorical and coordinate spatial representations: A reappraisal. *Memory & Cognition*, 20, 271–276.

- Schiller, P. H., & Malpeli, J. G. (1978). Functional specificity of lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, *41*, 788–797.
- Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, *79*, 3272–3278.
- Sergent, J. (1991). Judgments of relative position and distance on representations of spatial relations. *Journal of Experimental Psychology: Human Perception & Performance*, *17*, 762–780.
- Slotnick, S. D., Moo, L. R., Tesoro, M. A., & Hart, J. (2001). Hemispheric asymmetry in categorical versus coordinate visuospatial processing revealed by temporary cortical deactivation. *Journal of Cognitive Neuroscience*, *13*, 1088–1096.
- So, Y. T., & Shapley, R. (1979). Spatial properties of X and Y cells in the lateral geniculate nucleus of the cat and conduction velocities of their inputs. *Experimental Brain Research*, *36*, 533–550.
- Tovee, M. J., Rolls, E. T., Treves, A., & Bellis, R. P. (1993). Information encoding and the responses of single neurons in the primate temporal visual cortex. *Journal of Neurophysiology*, *70*, 640–654.
- Trujilli-Ortiz, A., Hernandez-Walls, R., Trujillo-Perez, R. A. (2004). RMAOV2: Two-way repeated measures ANOVA. Available from URL <http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=5578>.
- Van der Ham, I. J., van Wezel, R. J., Oleksiak, A., & Postma, A. (2007). The time course of hemispheric differences in categorical and coordinate spatial processing. *Neuropsychologia*, *45*, 2492–2498.
- Van der Lubbe, R. H., Scholvinck, M. L., Kenemans, J. L., & Postma, A. (2006). Divergence of categorical and coordinate spatial processing assessed with ERPs. *Neuropsychologia*, *44*, 1547–1559.
- Vidyasagar, T. R., Kulikowski, J. J., Lipnicki, D. M., & Dreher, B. (2002). Convergence of parvocellular and magnocellular information channels in the primary visual cortex of the macaque. *European Journal of Neuroscience*, *16*, 945–956.
- Weng, C., Yeh, C. I., Stoelzel, C. R., & Alonso, J. M. (2005). Receptive field size and response latency are correlated within the cat visual thalamus. *Journal of Neurophysiology*, *93*, 3537–3547.
- Wickelgren, W. A. (1977). Speed-accuracy tradeoff and information processing dynamics. *Acta Psychologica (Amsterdam)*, *41*, 67–85.
- Wickens, T. D. (2002). *Elementary signal detection theory*. New York, NY: Oxford University Press.
- Wilkinson, D., & Donnelly, N. (1999). The role of stimulus factors in making categorical and coordinate spatial judgments. *Brain & Cognition*, *39*, 171–185.
- Womelsdorf, T., Anton-Erxleben, K., Pieper, F., & Treue, S. (2006). Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nature Neuroscience*, *9*, 1156–1160.