Effect of the Number of Response Alternatives on Brain Activity in Response Selection

Sung-Ho Woo¹ and Kyoung-Min Lee^{1,2*}

¹*Interdisciplinary program of Cognitive Sciences, College of Medicine, Seoul National University, Chongno-Gu, Seoul, Korea*

²*Departments of Neurology, College of Medicine, Seoul National University, Chongno-Gu, Seoul, Korea*

Abstract: It is well-known in motor control literature that a response time (RT) increases as a logarithmic function of the number of response alternatives (NA) (Hick's law). In this study, we identified neural correlates for this relationship using event-related functional MRI and a choice finger-movement task. Behaviorally, average RTs of all subjects increased as a logarithmic function of the NA in accordance with the law. From a voxel-wise search for brain areas where the activity was correlated with NA and thence the RT, a positive correlation was found at the posterior cingulate and left superior frontal gyri, whereas a negative correlation was observed at areas in bilateral inferior parietal lobules. This differential modulation by the task context, namely, the NA available for a choice response with identical stimulus and response, indicates that these regions are involved in various aspects of response selection, intentional retrieval of motor program, or spatial expectancy. *Hum Brain Mapp* 28:950–958, 2007. ©2006 Wiley-Liss, Inc.

Key words: response selection; Hick's law; fMRI; information theory

INTRODUCTION

Generating an appropriate response to a stimulus is achieved via a series of information processing stages [Sternberg, 1969]. At least, three stages can be distinguished, namely, stimulus-identification, response selection, and response programming. Many factors have been proposed that can affect these stages: Clarity, intensity, and the pattern of stimulus arrangement influence the speed of stimulus identification.

Response selection takes longer when there are a larger number of alternatives (NA). In the response programming stage, factors such as complexity, duration, and accuracy of the movement play a crucial role [Schmidt and Lee, 1999].

Following Donder's hypothesis, it has generally been assumed that the time taken from stimulus presentation to action, i.e. the response time (RT), is a sum of the durations taken for the three mental processes. One can then infer the duration of a specific process and its characteristics by observing the changes in RT when factors affecting only the process are varied and those affecting other processes are kept constant.

For the selection of responses, Hick [1952] observed that RTs increased as a logarithmic function of the number of stimulus–response alternatives. His findings, known as Hick's law, can be described by the following mathematical formula: $RT = a + bH$, where $H = \log_2 (1/P_i)$, in which H is the amount of information that depends on the probability, P_i , of a stimulus event i [Schweickert, 1995]. Hick interpreted the relationship by making an analogy between human performance in choice decision tasks to that of an ideal communication system [Hick, 1952]. He argued that

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*Correspondence to: Kyoung-Min Lee, MD, PhD, Department of Neurology, Seoul National University Hospital, 28 Yongon-Dong, Chongno-Gu, Seoul 110-744, Korea. E-mail: kminlee@snu.ac.kr

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mean RT is linearly related to the average entropy of the signals because the system contains a communication channel of limited capacity through which all signals must pass. According to this theory, referred to as the communication theory by Laming [1968], it is the reduced probability of each alternative with more NAs, but not the actual NA, that determines RT. Later studies bolstered this notion by showing that, when alternative frequencies were unequal, RT changed approximately by the amount as predicted by the entropy measure of the probability changes [Crossman, 1953; Hyman, 1953]. More recently, Carpenter and Williams [1995] have demonstrated that saccadic latency varied as a logarithmic function of prior probability of a target being present, and further extended the same idea to a one-choice situation, claiming that the decision there was as to whether or not a target was present.

While the logarithmic relationship between RT and NA has been replicated in a substantial number of experiments, the communication theory of choice decision times has been seriously challenged from both theoretical and experimental perspectives [Luce, 1986, pp. 390–393 for a review]. For just one example of such criticisms, Laming [1968] pointed out that the basic conceptual framework of information theory entails the use of asymptotic theorems. Such theorems developed for an ideal communication system apply to set bounds in situations where a maximally efficient coding works on an indefinitely long sequence of signals. Since a subject must respond trial-by-trial in choice decision and cannot wait to take advantage of the long sequence of signals, one should not rely on the information theory and expect RT to be linear with entropy.

Given the inadequacy of Hick's original interpretation based on communication theory, many alternative accounts for Hick's law have been advanced. Christie and Luce [1956] postulated that the incoming signal is compared simultaneously with all possible identifications, and the decision to respond is taken when all the comparisons have been completed. Since the time taken by each comparison is subject to random variation, the larger the number to be made the greater the likelihood of one taking a long time and thus leading to a slow response. Laming [1966] generalized the mathematical formula for this parallel decision process model to $RT = a + b \sum 1/(r + k)$ where the summation runs from $r = 1$ to $r = NA$ and a , b , and k are constants to be determined from data. He showed that Hick's original data can be fit equally well by this equation. A second account for Hick's law was also proposed in the same paper where he pointed out that the above equation can be interpreted in terms of an epidemic model depicting the time taken for the spread of an epidemic [Laming, 1966]. This interpretation may prove fruitful if a more detailed model can be developed for a decision being made in a neuronal population as an outcome of spreading interactions among individual neurons of the population. Yet, another interpretation of Hick's law has recently been put forth by Usher et al. [2002]. The logarithmic increase in RT may be secondary to the requirement that

the response criterion be increased approximately logarithmically with NA to maintain a constant level of accuracy. The increase of the response criterion is so as to compensate for the increase in the likelihood that an incorrect alternative will be most active after any fixed amount of time accumulating information. Thus, they suggested that the use of a constant accuracy criterion is a general principle that leads to a logarithmic dependency of RT on NA for stochastic self-terminating models, which may apply equally well to sequential sampling models [Ratcliff and Smith, 2004; Smith and Ratcliff, 2004] and the LATER model [Reddi et al., 2003].

Recently, studies using electrophysiology and functional neuroimaging investigated brain activity involved in response selection. Basso and Wurtz [1997] found that, as the target uncertainty (i.e. the number of stimulus-response alternatives) increased, neural activity in the superior colliculus decreased, preceding target selection. It is quite possible that the change of NA modulate the activity of neurons in the cerebral cortex that are then projected down to the superior colliculus.

Deiber et al. [1991] addressed the question of the selection of movements. Changes in cortical activity associated with selection were monitored by measuring significant increase in regional cerebral flow with positron emission tomography. A comparison was made between tasks on which selection was required and a task in which the subjects made a single movement repetitively. When selection of a movement was made, significant increase in regional cerebral blood flow was found in the premotor cortex, supplementary motor cortex, and superior parietal association cortex. However, the selection required task was different from the repeated single-movement task from the aspect of complexity, content as well as selective processing. Therefore, the different activation obtained from control and experimental conditions seemed to include not only selective process but also motor planning and execution. In Schuster et al.'s [2001] PET study, greater activations with a choice RT task, when compared with a simple RT task, were found at the left prefrontal, premotor, and intraparietal areas, irrespective of whether the right or left hand was used. However, they did not consider a systematic variation of the NA in their experiments, but only compared the choice with the simple RT task. Moreover, the fact that responses were different in the two tasks—the index and middle finger movements for choice task versus only the index finger movement in simple response—made it impossible to rule out the possibility that factors influencing response programming rather than response selection had contributed to the results.

In our study, using event-related functional MRI imaging, we examined brain activity for a correlation with the variation of NA and RT. Since RTs in a choice RT task can also be influenced by other factors, such as stimulus dimensionality, discriminability, stimulus-response compatibility, and the modality of required responses, we kept them constant in our experiments.

Figure 1.

Stimuli and required responses. **A** represents one S-R alternative condition, **B** and **C** represent two and four S-R alternatives conditions, respectively. The red box indicates the trial conditions of the main comparison in the data analysis: The stimulus and response were identical and only the probability of a stimulus change, i.e. amount of information, was different across conditions. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

MATERIALS AND METHODS

Subjects

Ten participants (6 men and 4 women; aged 20–33 years, averaged 23.7) participated as volunteers in the present study, after giving an informed consent. All subjects were right-handed and had normal or corrected to normal visual acuity.

Behavioral Task

At the beginning of a trial, a white circular disc appeared in the center, to which subjects were instructed to focus their attention. After a delay of 1 s, the disc jumped to another location. Subjects' task was to detect the jump and respond by a button press with a finger as quickly and accurately as possible. Three conditions were specified across sessions by varying the possible directions of the disc jump. In one S-R alternative sessions, the disc always moved upward and the response was always made by an index finger. Thus, the probability of the upward jump is one and the information amount of the cue to respond was zero bit. Two S-R alternative sessions consisted of trials where the disc moved either up or

down, and responses were by the index or middle fingers, respectively. The probability of either cue was a half and the information one bit. For four alternative sessions, the right and left directions were added, for which the ring and little fingers were assigned as the response, respectively (Fig. 1 and Table I). Each cue was shown in a random sequence with a probability of one fourth and the information was two bits.

After a response, inter-trial interval was randomly varied ranging from 2 to 44 s (mean 11 s). The number of trials each participants received in 1-NA sessions was 16. To obtain the same number of trials with identical stimulus (upward jump of the disc) and response (index finger movement), the total number of trials in 2-NA sessions was twice, and that of 4-NA trials four times, as many as that of 1-NA trials. RTs were measured during fMRI image acquisition with an MR-compatible four-button keypad (Resonance Technology, Northridge, CA). Sixteen trials for each condition were given prior to scanning to learn stimulus–response association.

Imaging Parameters

Brain images were acquired using a GE Signa 1.5T MR scanner with a standard head-coil. T1-weighted anatomical

TABLE I. Experimental conditions

No. of alternatives	Stimulus	Required response	P	H
1	Up	Index finger pressing	1	0
2	Up/down	Index/middle finger	0.5	1
4	Up/down/right/left	Index/middle/ring/little	0.25	2

P , the probability of subsequent stimulus; H , the amount of information, which is equal to $\log_2(1/P_i)$.

images were obtained first (TR 500 ms and TE 12 ms), and then T2*-weighted EPI images at the same slice locations (154 brain volumes, TR 2000 ms, TE 60 ms, flip angle 90°, field-of-view $24 \times 24 \text{ cm}^2$, matrix size 64×64 pixels, 13 slices with a thickness of 5 mm separated by 2.5 mm, parallel to the AC-PC plane).

Data Analysis

SPM99 (Wellcome Department of Cognitive Neurology, London, UK) was used for realignment, Gaussian filtering, and spatial normalization of the brain volumes to the MNI templates. The data were then analyzed using BrainVoyager 2000 (Brain Innovation B.V., Maastricht, The Netherlands) for statistical analyses on individual and group data, based on the general linear model [Frackowiak et al., 1997]. Each conditional event was modeled using 1 s duration of box car function convoluted with a canonical hemodynamic response function. The group data were analyzed using a fixed-effect model to make statistical inferences.

Figure 2.

The performance (% correct) and RTs are plotted for each stimulus-response alternative condition. The mean and SE of the data over 10 subjects are shown.

The threshold for significance was set at $P < 0.05$ with the Bonferroni correction for multiple comparisons (Number of elements for the correction = 31,237). For the display of activated regions, the MNI coordinates were converted to the Talairach coordinates [Talairach and Tournoux, 1988].

RESULTS

Behavioral Results

Figure 2 shows the performance (percent correct) and RT in trials in which the cue stimulus was an upward shift and the correct response was a button-press using the index finger. The data were averaged over all subjects, and only correct trials were included to the calculation of the mean RT. Despite the fact that the cue stimulus and response were identical across all NA conditions, RTs increased as the function of the number of stimulus-response alternatives; the mean $\pm$ standard error (SE) was 407 ± 7 ms for 1 NA, 484 ± 9 ms for 2 NA, and 643 ± 11 ms for 4 NA condition. The slope of RT was 118 ms/bit, and the correlation coefficient, Pearson r , was 0.6456 ($P < 0.0001$), and r^2 was 0.4165. The mean percent correct was 100% (SE = 0) for 1 NA, $95 \pm 1.39\%$ for 2 NA, $97 \pm 1.47\%$ for 4 NA condition. There was no statistically significant correlation between the percent correct measure-

TABLE II. Areas that were activated in association with an index finger response across all conditions

Brain region	Coordinate			T score	N Vox
	x	y	z		
Lingual gyrus, BA 18/17	0	-79	-8	9.41	4,930
Right inferior parietal lobule, BA 40	52	-44	36	9.1	8,757
middle/inferior frontal gyrus, BA 46	41	46	7	8.85	4,396
Left inferior parietal lobule, BA 40	-46	-34	45	8.57	7,015
pre/postcentral gyrus, BA 4/2	-43	-20	54	7.14	4,153
Anterior cingulate, BA 32	1	24	24	7.1	1,510
Brain stem	1	-30	-5	6.8	2,406
Cunues, BA 7	1	-73	32	6.52	1,784
Thalamus	1	-6	1	6.03	538

The x , y , and z values show the center of gravity of the activated cluster in Talairach coordinate (the threshold for significance, $P < 0.05$ with Bonferroni correction for multiple comparison). N Vox indicates the size of activated cluster in the number of voxels.

Figure 3.

Brain regions that showed signal modulation in the index-finger trials across all NA conditions. The threshold for significance was set at $P < 0.05$ with Bonferroni correction for multiple comparisons. The number of elements for the correction was 31,237. Activated areas were superimposed on a template provided in BrainVoyager 2000. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

ments and the number of stimulus–response alternatives (correlation coefficient, Pearson r was -0.22 , $P > 0.2$).

Imaging Results

First, we identified regions that were activated in association with an index finger response across all conditions (Fig. 3 and Table II). These regions included the calcarine sulcus and the lingual gyrus (BA 17/18), the left pre- and postcentral gyri (BA 4/2), bilateral inferior parietal lobules

(BA 40), the middle and inferior frontal gyri (BA 46), and the anterior cingulate gyrus (BA 32).

Because our primary interest lied in the correlation between subjects' performance and brain activity, we used the difference of RT between each condition as the contrast weights and examined all brain voxels for those where the signal was correlated with the RT, either positively or negatively. In detail, the difference between the average RT of each condition and all condition was used as contrast weight for positive correlations and the reverse weight for negative correlations. Positive correlations, namely, greater

Figure 4.

Averaged percent change in BOLD signals in the lingual gyrus (A) and the pre- and postcentral gyri (B). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

TABLE III. Areas where the activity was positively correlated with the response time change

Brain region	Coordinate			T score	N Vox
	x	y	z		
Posterior cingulate gyrus, BA 23**	0	-58	16	5.29	274
Superior frontal gyrus, BA10/9**	-22	43	25	5.29	124
Right precentral gyrus, BA 6	50	-1	40	5.27	1,100
Anterior cingulate gyrus, BA 24	6	-9	39	4.61	52
Left parahippocampal gyrus, BA 34	-28	0	-15	4.47	239
Right parahippocampal gyrus, BA 28	29	-13	-12	4.24	303
Medial frontal gyrus, BA 6	5	-7	49	4.23	56
Left cuneus/precunues, BA 19/7	-12	-72	33	4.11	84
Left middle temporal gyrus, BA 39	-42	-67	14	4.08	93

**P < 0.05 with Bonferroni correction for multiple comparisons.

signals with longer RT, were found at areas in the posterior cingulate and right superior frontal gyri (Fig. 5 and Table III), and negative correlations (less signal with longer RT) in bilateral inferior parietal lobules (Fig. 6 and Table IV).

To examine temporal profiles of the BOLD signal, we chose six volumes of interest (VOI, $30 \times 30 \times 30$ cubic mm centered at the maxima in an activated cluster): (1) the lingual gyrus, (2) the pre- and postcentral gyri (these two areas were activated in all three NA conditions). The signal in these areas was not different significantly across NA conditions (see Fig. 4). In (3) the posterior cingulate gyrus and (4) the superior frontal gyrus, where a positive correlation of the signal with RT was observed, the signal decreased at the stimulus onset in the 1- and 2-NA conditions, but it remained at baseline or slightly increased in the 4-NA condition (see Fig. 5). In (5) the right inferior parietal lobules, where the activity was negatively correlated with RT, the signal was increased in the 1- and 2-NA conditions, but no significant change at the stimulus onset was observed in the 4-NA condition (Fig. 6A). In (6) the left inferior parietal lobule, where the activity was also negatively correlated with RT, the signal change at the stimulus onset was greatest in the 1-NA condition, and gradually less when the number of S-R alternatives was increased (Fig. 6B).

DISCUSSION

Our RT data showed an almost linear relationship with the amount of information of the stimulus (see Fig. 2). The slope in the log(NA)-RT plot was 118 ms/bit, which was higher than that from Hick's data. We believe this difference is attributable to a lack of practice in our experiment. In Hick's experiment, subjects practiced until the error rate came up to zero prior to the experiment, because Hick's main interest was in errorless performance. In contrast, our subjects practiced minimally before the scanning session. The level of practice is one of the variables that influence choice RT [Teichner and Krebs, 1974].

Areas Neural Activity Positively Correlated With S-R Alternative Increase

In the posterior cingulate, the activity decreased upon the cue onset when only one cue and response was expected, and it turned to a slight activation when more alternative cues were possible and the observed RT was longer. This is consistent with Badgaiyan and Posner's [1998] observation from an ERP study that the posterior cingulate activity was correlated with the load of response selection. They compared electrical potentials between generating the use of a noun (response selection) and reading a word aloud (simple repetition) and reported that the potential difference was best fit by dipoles located at the posterior cingulate. While the tasks that we and Badgaiyan et al. used were very different, a common feature was that subjects had to select from a set of possible stimulus-response associations in one condition and only one response was possible in the other. The cingulate is considered as part of an executive attention system, which is invoked when a supervisory mechanism is needed to resolve a cognitive conflict [Posner and Petersen, 1990]. A conflict may arise among competing alternative associations, but not when only one possible response is specified.

In the left superior frontal gyrus (BA 9/10, Talairach coordinates -22, 43, 25), brain activities during our choice task changed from a deactivation to the baseline, as the NA increased. In a study using word-stem completion tasks, Desmond et al. [1998] showed that the activity at the same location (Talairach coordinates -25, 44, 27) was greater when subjects completed word stems that had many possible answers than when the possible answers were only few. Although only one response was required for each word-stem, presumably more candidate words were activated and competed for selection when word-stems with many possible completions were given [Desmond et al., 1998]. This finding is in line with our results, together suggesting that the left frontal activity gets more activated when more items are retrieved from memory [Haxby et al., 1996; Roland and Guylas, 1995; Schacter et al., 1995] and the load for selection is greater.

Decary and Richer [1995] compared the performance of patients with frontal excisions, those with temporal excisions and control subjects in a task that required speeded choice responses, while manipulating perceptual difficulty,

TABLE IV. Areas which activity negatively correlated with response time increased

Brain region	Coordinate			T score	N Vox
	x	y	z		
Right inferior parietal lobule, BA 40**	55	-41	37	5.69	3,702
Left inferior parietal lobule, BA 40**	-52	-35	41	5.4	511
Right middle temporal gyrus, BA 21	53	-43	7	4.78	219
Superior frontal gyrus, BA 8	8	20	55	4.74	211
Right inferior frontal gyrus, BA 46	45	44	5	4.26	301

**P < 0.05 with Bonferroni correction for multiple comparison.

Figure 5.

Areas in which the activity was positively correlated with the RT and averaged percent change in BOLD signals. (A) is the posterior cingulate gyrus, and (B) is the superior frontal gyrus. BOLD signal changes were presented at right panel. Activated areas are overlaid on the MNI template brain MRI. The threshold for significance was set at $P < 0.05$ with Bonferroni correction for multiple comparisons. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

stimulus–response compatibility, and the NA. Frontal excisions were variable in extent but always included dorso-medial structures (anterior cingulate gyrus, superior frontal gyrus including supplementary motor area) and a variable amount of dorsolateral cortex anterior to the precentral sulcus. The NA was manipulated from 2 to 4. While the RTs of the three groups did not differ in the two-alternative task, the RTs of frontal patients were significantly longer than normal controls in the four-alternative task. The NA also exerted a significant group effect on error rates.

These findings suggest that the superior frontal gyrus is needed more when the NA increases, a notion that is consistent with our observation that the activity of the region is correlated with the NA.

Areas Neural Activity Negatively Correlated With an S-R Alternative Increase

In the right and left inferior parietal lobules, the brain activity changed from an activation state to baseline as the

Figure 6.

Areas with a negative correlation with RT and averaged percent change in BOLD signals. (A) is the right and (B) is the left inferior parietal lobule. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

number of stimulus–response alternatives increased; the inferior parietal lobules were activated in one- and two-alternative conditions, but not in the four-alternative condition. This negative correlation of the activity with alternative numbers may be related to the notion that the parietal region plays a role in directing attention [for reviews, see Kastner and Ungerleider, 2000]. In the one-alternative condition, there was only one possible spatial cue and one possible response. Therefore, subjects might have focused their attention only on one stimulus shift, i.e., an upward movement. In contrast, in the four-alternative condition, the probability of any one jump direction was lower, and therefore the spatial expectancy would have been weaker and the parietal activity lower.

This situation is somewhat similar to the experiment conducted by Vandenberghe et al. [2001]; in their study, a feature-based cue led to a global expectancy of targets on either side of the visual space, whereas a location-based cue elicited a more focal expectancy, which was limited to only one side. They observed that the right inferior parietal lobule showed a significantly higher activity, when the task was performed based on the location rather than the feature of a stimulus, and concluded that the activity was related to the spatial expectancy. Similarly, the activity of inferior parietal cortex in our experiments might have been modulated by spatial expectancy; when the probability of a particular stimulus shift was high as in one- or two-alternative conditions, the expectation of a shift toward one location was high as well, which might have led to the activation of the right inferior parietal area. On the other hand, when the probability of a particular stimulus shift was low, the correct expectation of a shift was neither possible nor necessary, and hence less activation of the parietal cortex. Therefore, it is quite possible that the negative correlation of the parietal activity with NA could be mediated by the process of expecting an event at a particular location and focusing attention there in advance.

The involvement of the parietal cortex in the selection of motor programs is supported by a large body of clinical literature pertaining to apraxias. In these conditions, especially the ideational/conceptual apraxia, patients experience difficulties in choosing an appropriate motor act, when given an object or a verbal cue. However, whether their impairment is related to the NA choices is not clear in the literature. Therefore, while the negative correlation of parietal activations with alternative numbers is possibly related to the process of motor program selection, the relationship doesn't seem straightforward, and needs further investigation.

In summary, we observed that during response selection, a large-scale cortical network gets activated, including the posterior cingulate gyrus, left superior frontal gyrus, and bilateral inferior parietal lobules and that the activations were influenced by NA: In the frontal and cingulate areas, brain activity increased, while the activity decreased in the parietal areas, as the NA and the RT increase. These findings are consistent with a general concept emerging

from functional neuroimaging that a cognitive task is subserved by a large-scale cortical network that consists of spatially separate components, each with its own relative specialization, that collaborate extensively to accomplish a cognitive function [Just et al., 1999].

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