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Contributions of the left and right hemisphere to ratio scaling.

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CONTRIBUTIONS OF THE LEFT AND RIGHT HEMISPHERE
TO RATIO SCALING

by

TRACY S. KRETZMER

A DISSERTATION

Submitted to the graduate faculty of The University of Alabama at Birmingham,
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

BIRMINGHAM, ALABAMA

2006

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ABSTRACT OF DISSERTATION
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Title Contributions of the Left and Right Hemisphere to Ratio Scaling

This paper examines whether ratio scaling, the principle behind the psychophysical Power Law, is equal for stimulus magnitudes presented to the left and right cerebral hemispheres and how magnitude estimates are integrated between hemispheres. Three models of hemispheric integration were tested (dominance, summation, and inhibition) by using a cross-modal matching procedure in right-handed male subjects. Visual stimuli were presented to one or both hemispheres by using a tachistoscopic method to test all three models. Olfactory stimuli were also presented to one or both nares (hemispheres) to test the dominance and summation models. A dominance model was not supported, as there was little in ratio scaling difference between hemispheres for either visual or olfactory stimuli. Olfactory integration followed a summation model, but visual stimuli did not. Inter-hemispheric inhibition did not account for hemispheric integration in the visual modality. Instead, the most interesting findings stemmed from within, rather than between, hemisphere comparisons. Ratio scaling parameters appeared to be driven by the amount of stimulation provided, whereas variability in ratio scaling corresponded to whether the two hemispheres received equal amounts of stimulation. We conclude that, stimulus induced cerebral activation influences both the form and fit of power functions used to characterize ratio scaling.

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INTRODUCTION

Magnitude estimation is a method of ratio scaling in which subjects are asked to rate the intensity of suprathreshold sensory stimuli. This is done by either numerical matching, reproducing stimulus magnitudes (magnitude production) or by matching the intensity of one type of stimulus to that of another (cross-modal matching) (Stevens, 1975a). According to Stevens (1975a), the principle behind the Power Law is ratio scaling, in that “equal stimulus ratios produce equal sensation ratios” (p. 14). In turn, ratio scaling is mathematically expressed as a power function, which summarizes the ratio at which perceived magnitude “grows” in response to the ratio of change in objective stimulus magnitude. The wide application of the power law, spanning perceptual and social judgment, suggests that ratio scaling is an organizing principle of the peripheral and central nervous systems, which interact to construct mental representations of stimulus magnitude (Mennemeier et al., in press).

Ratio scaling is characterized for a given perceptual continuum (type of stimulus) by the form of the power function (the size of the exponent and constant) that relates subjective and objective measures of stimulus intensity (Stevens, 1975a). Power functions are derived by log-transforming data to make them linear and regressing estimates of magnitude on objective measures of stimulus intensity. The power function exponent is equal to the slope of the regression line, and the constant is equal to the y-intercept (Stevens, 1975). The r^2 value is a measure of variability indicating how well data fit a power

function. Power function parameters can be compared between individuals, groups, or experimental conditions to evaluate associated differences in ratio scaling.

Altered ratio scaling in the form of magnitude estimation and production has been linked to right-hemisphere injury, particularly in patients with unilateral neglect (Chatterjee, 1995; Chatterjee, Dajani, & Gage, 1994; Chatterjee, Mennemeier, & Heilman, 1992b, 1994; Mennemeier, Rapcsak, Dillon, & Vezey, 1998; Mennemeier, Vezey, Lamar, & Jewell, 2002; Mennemeier et al., in press). Neglect is defined as the failure to report, respond to, or act upon stimuli located contralaterally to brain injury (Heilman, Watson, & Valenstein, 1985). Although neglect is associated with damage to the fronto-cingular-temporoparietal network implicated in spatial attention (Heilman, Watson, & Valenstein, 1994; Karnath, Ferber, & Himmelbach, 2001; Karnath, Himmelbach, & Rorden, 2002; Mesulam, 1981; Vallar & Perani, 1987), it is most common, severe, and persistent following right-hemisphere lesions. Neglect has, less commonly, also been shown to follow left-hemisphere injury (Ringman, Saver, Woolson, Clarke, & Adams, 2004).

Patients with right-hemisphere injury and neglect produce power functions with lower exponents and higher constants than either normal control subjects or patients without neglect produce (Chatterjee, 1995; Chatterjee, Dajani, & Gage, 1994; Chatterjee, Mennemeier, & Heilman, 1992a; Chatterjee et al., 1992b; Mennemeier et al., 2002; Mennemeier et al., in press). A decreased exponent and an increased constant suggest a restricted range of magnitude estimates (Cross, 1973; Hollingworth, 1909), such that lesser stimuli in a range are overestimated and greater stimuli are underestimated. Additionally, magnitude estimates in neglect patients are more variable than they are in normal patients or patients without neglect, as indicated by a decrease in their r^2 value relative to those of

other groups (Mennemeier, Murphy, Kretzmer, Jewell, & Nunn, 2003). Finally, ratio scaling may also be altered by left-hemisphere injury (Woods et al., in press); however, like neglect, it is less frequently observed and may be qualitatively different from that seen after right-hemisphere injury. Although the power function exponent is typically decreased in these patients, the constant may be increased or decreased relative to that of normal subjects.

A review of data from neurophysiological and neuroimaging studies in both humans and animals (Walsh, 2003) posited a common “magnitude system” for estimates of space, time, and quantity localized to the inferior parietal cortex of the right-hemisphere. Quantity judgments, in particular, correspond to a class of perceptual continua (prothetic) that conform to ratio scaling (Stevens, 1971). In contrast, a functional MRI study of comparative magnitude estimates concerning number, size, and luminance in normal subjects (Pinel, Piazza, Biham, & Dehaene, 2004) found evidence for bilateral cerebral activation localized to the intraparietal sulci and precentral and occipitotemporal areas. Data from these studies converge with those of brain-injured subjects to suggest that both cerebral hemispheres engage in ratio scaling but may play different roles. The purpose of this study was to test three models by which magnitude estimates formed in each hemisphere are combined.

The first model, a right-hemisphere dominance model for ratio scaling, predicts that power functions generated by the right-hemisphere are qualitatively different from those generated by the left-hemisphere. Because exponents are decreased and because constants are increased after right-hemisphere injury (Chatterjee, Danjani & Gage, 1994; Chatterjee, Mennemeier, & Heilman, 1994; Mennemeier et al., 2003), we predicted that

the right-hemisphere normally generates higher exponents and lower constants than the left-hemisphere does. This is plausible because the exponents and constants derived from most patients with left-brain injury are not different from those of normal subjects (Mennemeier, et al., 2003; Mennemeier, et al., in press). In other words, the “normal” exponent and constant for a given continuum may reflect a greater contribution of the right than of the left-hemisphere.

Alternatively, the two hemispheres may perform ratio scaling equally well, and integration may follow a summation model. Stevens (1975a) and Stevens and Galanter, (1957) observed that when sounds are presented simultaneously to both ears versus to one ear alone, subjects report not a doubling of the loudness but a fractional increase in loudness that depends on initial stimulus intensity. This pattern of summation is denoted by an increase in the size of the power function constant without a change in the size of the exponent. Ratio scaling is not altered; instead a general increase in perception of stimulus intensity occurs. A summation model of hemispheric integration would be consistent with Pinel and colleagues’ (2004) findings but not with data from brain-injured patients, which are more consistent with a dominance model for ratio scaling.

Interhemispheric inhibition provides a third model of how estimates of stimulus magnitude may be integrated between hemispheres and how perception of stimulus magnitude is altered after left- and right-hemisphere injury. The two cerebral hemispheres are viewed as mutually inhibitory of each other (Heilman & Van Den Abell, 1980; Kinsbourne, 1970); however, it is not clear which hemisphere exerts a greater inhibitory influence when the stimulus environment creates competition between hemispheres. Heilman and Van Den Abell (1980) proposed that the right-hemisphere is dominant for attention

because it is activated by novel visual stimuli in both the left and right hemispatial fields, whereas the left-hemisphere is activated only by stimuli in the right hemispatial field. In contrast, Kinsbourne (1970) argued that the left-hemisphere is normally more inhibitory of the right than the right is of the left.

In addition, interhemispheric inhibition may be magnified by unilateral brain injury. For example, extinction occurs after unilateral brain injury when a stimulus delivered to one side of the body is not perceived because a competing stimulus is delivered to the opposite side of the body (Heilman et al., 1985). Extinction is common in patients with neglect and almost certainly involves inhibition of one hemisphere by the other (Reider, 1946). A positron emission tomography study of competing stimuli presented in both visual hemifields (Fink, Driver, Rorden, Baldeweg, & Dolan, 2000) showed reduced activation of striate and extrastriate visual cortex when competition between hemispheres was present and greater activation when competition between hemispheres was absent. Furthermore, a rapid-rate transcranial magnetic stimulation (rTMS) study of visual extinction found that occipital rTMS led to a large number of misses for contralateral targets presented both singly and bilaterally, whereas parietal rTMS did not cause misses on single stimuli but did lead to a large number of contralateral misses for bilateral stimuli (Pascual-Leone et al., 1994). Damage to the fronto-cingular-temporoparietal network in one hemisphere may have an effect similar to that of rTMS, except the damaged hemisphere is also actively inhibited by the intact hemisphere when both are stimulated simultaneously. It follows that extinction may not be confined to threshold stimuli but may apply as well to ratio scaling for suprathreshold stimuli. In a case study of neglect, Chatterjee, Thompson, and Ricci (1998) found that the power function relationship for estimates

of weights lifted with the hand contralateral to brain injury was obliterated when the patient also lifted weights with the ipsilateral hand. In other words, ratio scaling was extinguished by activation of the intact hemisphere.

In contrast, we would not expect to find extinction in healthy controls because of intact hemispheric integration processes. However, research has demonstrated a partial form of extinction called obscuration in normal subjects (Benton & Levin, 1972). Benton and Levin observed that the obscuration method of Jacob Loeb (1885) provided a model of interhemispheric inhibition for normal subjects. Their method used double simultaneous stimulation, as in extinction techniques, except a stronger stimulus was applied to one side of the body to induce suppression of a weaker stimulus applied on the opposite side. Healthy controls were asked to rate weights ranging from 1 to 20 g. These target weights were presented to either the left or the right forearm unilaterally. Subjects also rated the weight of stimuli when a 40 g weight was presented simultaneously on the opposite side of the body. Obscuration stimuli led to a reduction in estimates of weight relative to when stimuli were rated without obscuration stimuli. In other words, obscuration stimuli presented to one side of the body inhibit estimates of stimulus magnitude for stimuli presented on the opposite side of the body. As a result, Benton and Levin concluded that extinction and obscuration were exaggerated expressions of a normal neural mechanism.

The obscuration method was used in this study to test an interhemispheric inhibition model of the integration of ratio scaling between hemispheres. For example, the right-hemisphere might normally contribute more to ratio scaling, not because it generates different power functions than the left does, but because its activation by novel environmental stimuli causes inhibition of the left-hemisphere. If so, presenting obscuration

stimuli to the left-hemisphere should counteract this effect (cause right-hemisphere inhibition), whereas presenting obscuration stimuli to the right-hemisphere should enhance this effect (enhancing left-hemisphere inhibition). A result in the opposite direction would favor Kinsbourne's (1970) assertion that the left-hemisphere normally exerts a greater inhibitory influence on the right than the right-hemisphere normally exerts on the left.

Models of hemispheric integration for ratio scaling were tested by presenting stimuli either to one hemisphere (unilateral presentation) or to both hemispheres simultaneously (bilateral presentation). Two sensory modalities, visual and olfactory, were used. Visual stimuli were presented by using tachistoscopic methods, which allow the "loading" of sensory information more directly into one hemisphere (Iaccino, 1993; McKeever, 1986). Olfactory stimuli were presented by using odor sticks. The use of olfactory stimuli takes advantage of the fact that the olfactory pathways are ipsilateral (Cain, 1977; Koelega, 1979; Yougentob, Kurtz, Leopold, Mozell, & Hornung, 1982); therefore, as is the case with tachistoscope, presenting stimuli to one naris loads the ipsilateral hemisphere with olfactory stimulation. Subjects rated stimuli presented to one hemisphere by using the contralateral hand (a cross-modal matching method) to preserve compatibility between hemisphere presentation and hand rating. Because this study examined hemispheric contributions to ratio scaling, right-handed male subjects were recruited specifically to emphasize any lateral asymmetries that might be found. Lateralized differences in stimulus processing are exhibited to greater degrees in both males and right-handers (Bryden, 1973, 1979; Kimura, 1969; McGlone, 1978; McKeever, Van Deventer, & Suberti, 1973). A right-hemisphere dominance model would be supported if,

during unilateral presentations, exponents generated by the right-hemisphere were greater and constants were lesser than those generated by the left-hemisphere were found to be. A summation model for hemispheric integration would be supported if, during bilateral stimulus presentations, an increase in the constant but not the exponent was observed. Finally, Heilman (1979) and Kinsbourne's (1970) models of interhemispheric inhibition were tested by using obscuration stimuli as described above.

METHOD

Participants

Forty-four right-handed volunteers from the University of Alabama at Birmingham participated in the experiment and ranged in age from 18-35 years (22.4 ± 4.8). Right-handedness was defined as a score greater than 75% on the 10-item Edinburgh Handedness Inventory (Oldfield, 1971). This study was approved by the Institutional Review Board for Human Use (see appendix A) and all participants gave informed consent before study inclusion. All participants had normal or corrected-to-normal vision in both eyes as measured by the Lighthouse Distance Visual Acuity Test, 2nd edition, eye chart. Additional exclusion criteria included current acute psychiatric symptomology, history of neurological abnormalities, anosmia, or hyposmia.

Apparatus and stimulus materials

Visual Magnitude Estimation. Visual stimuli to be estimated consisted of eight solid black squares varying in size from 4.5 to 14.0 cm. A total of 132 stimulus slides were used in three separate paradigms: a) bilateral, b) unilateral, and c) obscuration.

Stimuli were presented to participants by using a Lafayette 43016 shutter control tachistoscope with a 100 ms timer to control stimulus duration and a Kodak Ektragraphic IIIe Plus slide projector with an MKO zoom (100-150 mm) lens. A black dot with a diameter of 1.0 cm was placed at the center of the screen as a fixation target. To ensure

consistent head orientation, a chin rest was bolted at the opposite end of a table directly in front of the screen.

Each participant was asked to rate the intensity of each visual stimulus by turning a dial with his right hand and left hand (see Figure 1). This procedure eliminates a verbal response, which can activate the left-hemisphere. Dial turns were recorded using with a transducer that displayed a number on an LCD screen out of visual range of the participant.

Olfactory Magnitude Estimation. To prevent retronasal smelling and trigeminal excitation, the odorant phenyl-ethylalcohol (PEA) was chosen (Doty et al., 1978; Kobal, Hummel, & Pauli, 1989). Five concentrations of PEA, ranging from 0.78% to 100%, were presented to each participant. Burghart's "Sniffin' Sticks" kit was used to dispense PEA odorants. Sniffin' Sticks are sealed odorant-containing pens used to test olfactory performance (Kobal et al., 1996). Participant responses were produced as before with a dial turn.

Procedure

Visual Magnitude Estimation. Participants were seated upright in straight-backed chairs 113 cm in front of the projection screen with their chins in the rest. Before to experimental trials, each participant was instructed to focus on the fixation point. They were specifically told not to deviate from fixation. To ensure fixation, the subject's eyes were recorded from an aperture in the fixation point and monitored on a TV screen. Trials were

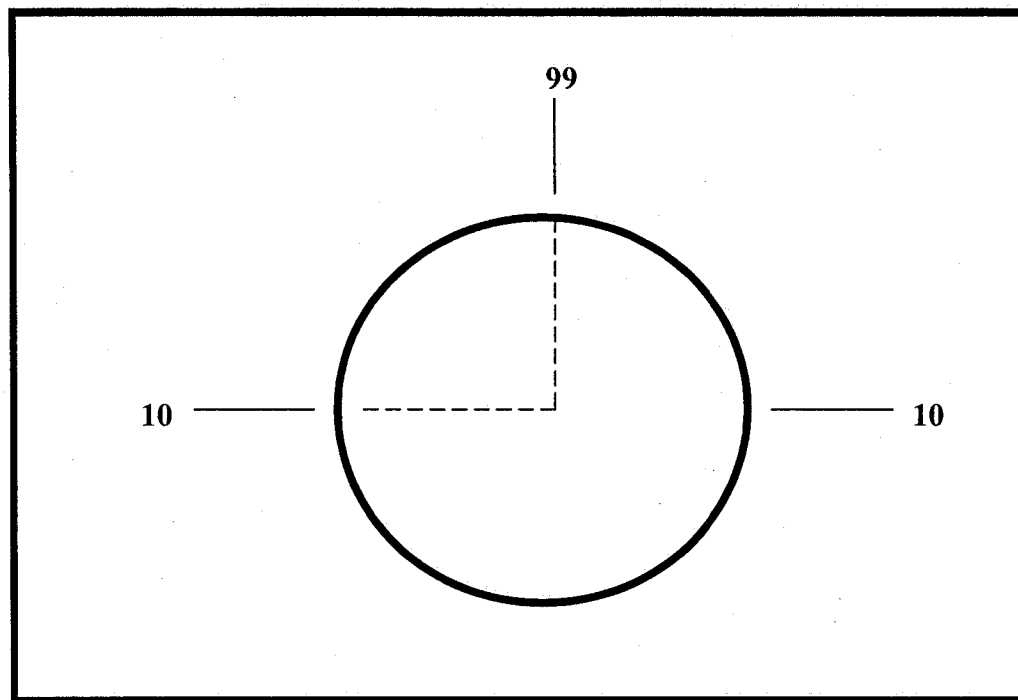


Figure 1. Motor rating dial apparatus. Dial has separate right and left 90° rotation ranges. During right-handed responses, the left side of dial represented lower intensity ratings, and the midline represented higher intensity ratings. This rating scale was reversed for left-handed responses, with the right side of the dial representing lower intensity ratings and with the midline reflecting higher intensity ratings.

readministered if the participants' gaze deviated from the central fixation point. Before to each stimulus presentation, participants were instructed to focus on the fixation stimulus. After 500 ms the stimulus was presented for 100 ms. Participants were instructed to maintain their focus on the fixation point even during target stimulus presentation. After stimulus presentation, participants were asked to rate stimulus intensity. Redirection of center fixation was stated before each trial. To familiarize the participants with the procedure, 16 practice trials were given before formal testing. Failure to discriminate large area differences in terms of either using the dial (i.e., turning the dial farther for larger area trials vs. turning the dial less for smaller area trials) or making verbal responses (i.e., stating whether the area box was smaller or larger than the previous slide shown) after 16 practice trials resulted in participant elimination. Two participants were excluded for this reason.

Before stimuli presentation, participants were instructed on cross-modality matching methodology. They were instructed to turn the dial, within a 90° radius to match the size of the square with either their left or their right hand. During right-handed responses, the left side of dial represented lower intensity ratings, and midline represented higher intensity ratings. This rating scale was reversed for left-handed responses, with the right side of the dial representing lower intensity ratings and midline reflecting higher intensity ratings (see Figure 1).

Visual stimuli were randomly presented in three separate paradigms: a) bilateral, b) unilateral, and c) obscuration (see Figure 2). Each paradigm was presented twice, once to record right-hand responses (RHRs) and once to record left-hand responses (LHRs). To control for order effects, RHRs and LHRs were counterbalanced across all stimuli,



Figure 2. Tachistoscopic magnitude estimation paradigms. Area stimuli for bilateral, unilateral, and obscuration paradigms.

paradigms, and participants. Right unilateral, left unilateral, and bilateral stimuli consisted of eight area magnitudes presented randomly in separate blocks, for a total of 24 magnitude estimations each. Stimuli were projected at a distance of 4.0 cm from the center of the fixation point to the center edge of the stimuli, thus subtending a visual angle of 5° .

Obscuration trials consisted of one of six target stimuli, ranging from 4.5 to 8.5 cm on one side of the fixation point and one modulus stimulus measuring 14 cm on the opposite side of the fixation point. A total of 12 slides were used, with 6 target-right slides and 6 target-left slides presented three times each (see Figure 2).

Olfactory Magnitude Estimation. Participants were required to not eat or drink anything except water for 15 min before odorant exposure. Participants were instructed to rate the magnitude of each presented stimulus via the cross-modality matching procedures discussed above. Each of the five concentrations was randomly presented in three separate blocks, with a brief resting interval of 2 min before the next block was presented. Olfactory presentations included separate bilateral and unilateral paradigms. For bilateral odor presentation, each of the concentrations was placed approximately 2 cm under each naris for 3 s. To prevent environmental odor contamination, the examiner wore disposable odorless gloves. Intervals of at least 30 s between trials were provided to prevent olfactory desensitization (Hummel et al., 1997). Participants were free to sample the odors as often as necessary. Responses were recorded with separate RHR and LHR procedures. For unilateral trials, odorant pens were presented to either the left or the right naris exclusively. To ensure unilateral presentation, the participant's contralateral naris

was occluded with 3M Microfoam surgical tape. Because of ipsilateral pathways, participants were instructed to respond with the contralateral hand only.

Statistical Analysis

Each participant's ratings were regressed onto actual stimulus intensity to yield separate exponent, constant, and r^2 values (see Table 1). A significant r^2 value indicated that the data fit power functions. Power functions were calculated with the SPSS v.11 package. The SAS v.9 package was used to conduct repeated-measure analyses with specific contrasts to examine each model proposed.

Table 1

Mean Exponents, Constants and r^2 for Group Visual and Olfactory Paradigms

Paradigm	Exponent X (SD)	Constant X (SD)	r^2 X (SD)
Area Bilateral Right Hemisphere	1.05 (0.34)	6.24 (3.88)	.79 (.07)
Area Bilateral Left Hemisphere	0.97 (0.32)	6.12 (3.44)	.79 (.08)
Area Unilateral Right Hemisphere	0.94 (0.29)	7.69 (4.82)	.75 (.12)
Area Unilateral Left Hemisphere	0.91 (0.35)	9.04 (6.14)	.73 (.10)
Obscuration Right Hemisphere	1.15 (0.47)	5.90 (5.60)	.70 (.18)
Obscuration Left Hemisphere	1.07 (0.45)	6.91 (5.37)	.73 (.15)
Olfactory Bilateral Right Hemisphere	0.23 (0.10)	25.46 (11.48)	.71 (.16)
Olfactory Bilateral Left Hemisphere	0.23 (0.10)	24.31 (9.64)	.72 (.12)
Olfactory Unilateral Right Hemisphere	0.22 (0.10)	21.65 (8.74)	.64 (.17)
Olfactory Unilateral Left Hemisphere	0.24 (0.10)	19.49 (8.84)	.72 (.12)

Note. Results based on $n = 20$ (visual correlations) and $n = 31$ (olfactory correlations).

RESULTS

Participants

Power functions not reaching significance ($r^2 < .05$) were not analyzed. This excluded 2 participants from the visual data set and 9 participants from the olfactory data set. To ensure that power functions generated from the visual and olfactory experiments accounted for roughly equal portions of variance, power functions yielding extreme r^2 values, as defined by values greater than 1.5 times the interquartile range within each paradigm, were eliminated from further analyses. This resulted in a loss of 3 additional participants from the visual data set and 1 from the olfactory data set. Finally, 4 more participants were excluded from the visual data set because of missing values (a requirement for the repeated-measures procedure). In the end, the visual data set was composed of 20 participants (20 participants for the obscuration analyses) and the olfactory data set was composed of 31 participants.

Right-Hemisphere Dominance Model

The size of power function exponents and constants were not different between hemispheres during unilateral stimulus presentations for either visual or olfactory stimuli.

Summation Model

Paired contrasts demonstrated significant differences between right-hemisphere visual bilateral (1.05 ± 0.34) and unilateral (0.94 ± 0.29) ($F = 6.96, p = .02$) exponents and between bilateral (6.24 ± 3.88) and unilateral (7.69 ± 4.82) ($F = 4.99, p = .04$) constants.

Analyses of left-hemisphere bilateral trials versus left-hemisphere visual unilateral trials demonstrated no significant differences in exponent sizes. However, significant differences were found for the constants between left-hemisphere bilateral (6.12 ± 3.44) and left-hemisphere unilateral conditions (9.04 ± 6.14) ($F = 5.79, p = .03$); these differences were in the same direction as that observed for the right-hemisphere.

No significant differences were found between olfactory bilateral and unilateral exponent sizes regardless of cerebral hemisphere. Right-hemisphere comparisons revealed significantly higher bilateral constant sizes (25.46 ± 11.48) than unilateral constant sizes (21.65 ± 8.74) ($F = 7.04, p = .01$). Left-hemisphere comparisons also demonstrated significant differences in the same direction between bilateral (24.31 ± 9.64) and unilateral constant sizes (19.49 ± 8.84) ($F = 15.51, p = <.001$).

Inhibition Model

Comparative analyses did not demonstrate significant differences in either exponents or constants between right and left obscuration trials.

Furthermore, exponents and constants for obscuration trials were also compared to those for bilateral and unilateral stimulus presentation trials. Paired contrasts did not reveal differences between right-hemisphere bilateral trials and right-hemisphere obscu-

ration trials (left-hemisphere receives obscuration stimulus and right-hemisphere receives stimulus to be rated) in the size of either the exponent or the constant. However, right-hemisphere unilateral trials yielded significantly lower exponents (0.94 ± 0.29) and significantly higher constants (7.69 ± 4.82) than right-hemisphere obscuration trials for the exponents (1.15 ± 0.47) ($F = 8.71, p = .008$) and constants (5.90 ± 5.60) ($F = 4.24, p = .05$).

Similar contrasts for the left-hemisphere revealed lower exponents (0.97 ± 0.32) and lower constants (6.12 ± 3.44) during bilateral trials than during obscuration trials (exponents $1.07 \pm 0.45, F = 183.6, p < .001$; constants $6.91 \pm 5.37, F = 65.24, p < .001$). Additionally, unilateral exponents were lower (0.91 ± 0.35) and constants were higher (9.04 ± 6.14) than during obscuration trials (exponents $1.07 \pm .45; F = 7.44, p = .01$) (constants $6.91 \pm .537; F = 6.26, p = .02$).

r² Correlations

Correlations between r^2 and exponent and constant values were calculated for both visual and olfactory paradigms (see Table 2). In bilateral trials, r^2 values did not share significant variance with exponent and constant values for area judgments. In contrast, both unilateral and obscuration comparisons yielded higher r^2 values, indicating significant correlations with both exponent and constant values.

In olfactory comparisons, r^2 values were significantly correlated with bilateral and unilateral exponents. However, with the exception of olfactory bilateral right-hemisphere, r^2 values did not share significant variance with constant values in olfactory comparisons.

Table 2

r² Correlations with Exponent and Constant Values

Paradigm	Exponent		Constant	
	<i>r²</i>	<i>p</i> value	<i>r²</i>	<i>p</i> value
Area Bilateral Right Hemisphere	.282	.228	-.250	.287
Area Bilateral Left Hemisphere	.263	.262	-.125	.598
Area Unilateral Right Hemisphere	.597	.005	-.495	.026
Area Unilateral Left Hemisphere	.636	.003	-.635	.003
Obscuration Right Hemisphere	.705	<.001	-.838	<.0001
Obscuration Left Hemisphere	.516	.020	-.581	.007
Olfactory Bilateral Right Hemisphere	.506	.004	-.419	.019
Olfactory Bilateral Left Hemisphere	.375	.038	-.180	.333
Olfactory Unilateral Right Hemisphere	.612	.0003	-.235	.203
Olfactory Unilateral Left Hemisphere	.631	.0001	-.136	.465

Note. Results based on $n = 20$ (visual correlations) and $n = 31$ (olfactory correlations).

DISCUSSION

Three models of hemispheric integration for ratio scaling were tested in this study to further investigate how magnitude estimates are formed and integrated by the two cerebral hemispheres. A dominance model predicts increased power function exponents and decreased constants for the right-hemisphere when compared to those for the left-hemisphere during unilateral stimulus presentation. A summation model predicts increased constants for both hemispheres in bilateral versus unilateral stimulus presentations. Finally, an interhemispheric inhibition model predicts altered ratio scaling in one hemisphere when the other hemisphere receives an obscuration stimulus.

Studies of ratio scaling in brain-damaged patients (Chatterjee, 1995; Chatterjee et al., 1994; Chatterjee, Mennemeier, & Heilman, 1994; Mennemeier et al., 1998, 2002, in press), and in normal subjects and animals (Walsh, 2003) suggest a right-hemisphere dominance model. In contrast, a functional MRI study (Pinel et al., 2004) of normal subjects suggested bilateral cerebral activation during ratio scaling. Our results did not support a right-hemisphere dominance model for ratio scaling. In fact, none of the findings indicated a difference in ratio scaling between hemispheres in this study. Results were surprisingly uniform even for comparisons within hemisphere. For example, the effect size to detect a change in the exponent between unilateral and bilateral visual stimulus presentations was 0.32 for the right-hemisphere and 0.22 for the left-hemisphere, whereas the effect size to detect a change in the constant was 0.43 for the right-hemisphere and

0.55 for the left-hemisphere. For olfactory stimuli, the effect size to detect a change in the constant between unilateral and bilateral olfactory stimulus presentations was 0.37 for the right-hemisphere and 0.52 for the left-hemisphere. Therefore, the two hemispheres appear equally adept at ratio scaling.

How then does one explain the rather strong empirical support for a right-hemisphere dominance model for ratio scaling? Although the right-hemisphere may not contribute more to ratio scaling than the left-hemisphere does, it may be more susceptible to factors that influence ratio scaling, like cerebral activation and unequal stimulus presentation. The right-hemisphere appears to play an important role in arousal (Heilman & Van Den Abell, 1980; Robertson, 2001) and thus may be more susceptible to activation by environmental stimuli. Because the right-hemisphere has receptive fields for visual stimuli in both left and right hemifields (Corbetta, Meizin, Shulman, & Peterson, 1993; Heilman & Van Den Abell, 1980), it may also be more subject to cerebral activation and therefore more sensitive to differences in stimulation between the hemispheres. A study by Coslett, Bowers and Heilman (1987) demonstrated that individuals with right-hemisphere damage were significantly more impaired in their capacity for cerebral activation than individuals with left-hemisphere damage were found to be. Coslett et al.'s findings indicate that right-hemisphere damage may result in performance deficits because the capacity for cognitive activation is limited. These findings have further implications for the rather strong empirical support for a right-hemisphere dominance model for ratio scaling. Neglect is often described as a disorder of attention and arousal (Heilman, 1979; Heilman & Valenstein, 1972; Mesulam, 1981; Watson, Heilman, Cauthen & King, 1973). It follows, that because the level of arousal is a major determinant of the capacity

for cerebral activation, then one would predict a positive correlation between the presence of neglect and an impaired capacity for cognitive activation. Therefore, when neglect patients demonstrate impaired ratio scaling, these deficits reflect a diminished capacity for cerebral activation. Further work is necessary to understand these processes, but they could explain why right-hemisphere damage compromises ratio scaling more than damage to the left hemisphere does.

The summation model, tested by comparisons between bilateral and unilateral presentations, was supported only within the olfactory paradigm. The finding of increased bilateral constants (right and left-hemisphere) relative to unilateral constant sizes, without a change in the size of the exponent, reflects a general increase in perceived stimulus intensity, rather than a change in ratio scaling (see Figures 3 and 4). Our results converge with those of electrophysiological studies of olfaction. Early olfactory studies demonstrated that, when odor was presented birhinally, a summation of impulses occurred rather than a doubling of monorhinal impulses (Eisberg, 1935, 1936). Although Eisberg's (1935, 1936) research provides similar results, methodological differences (cross-modal matching vs. electrophysiological impulses) between those studies and our study allow us to draw only tentative conclusions. According to Bensafi and colleagues (2004), differences in airflow rate and odorant sensitivity between the nostrils produce disparate images of the olfactory world to each hemisphere. How the hemispheres integrate information into a unified olfactory percept is still unknown. Our results, however, in addition to Eisberg's findings seem to indicate a summation process of olfactory integration. However, further work is needed.

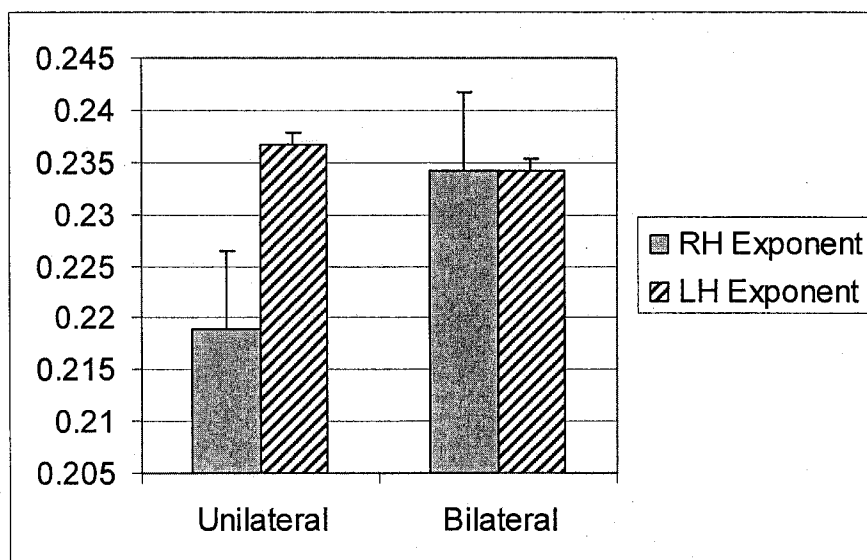


Figure 3. Mean olfactory exponents bar graph. Bar graph showing mean and standard error (+1 *SE*) of olfactory exponents across paradigms ($n = 31$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere; LH = left hemisphere.

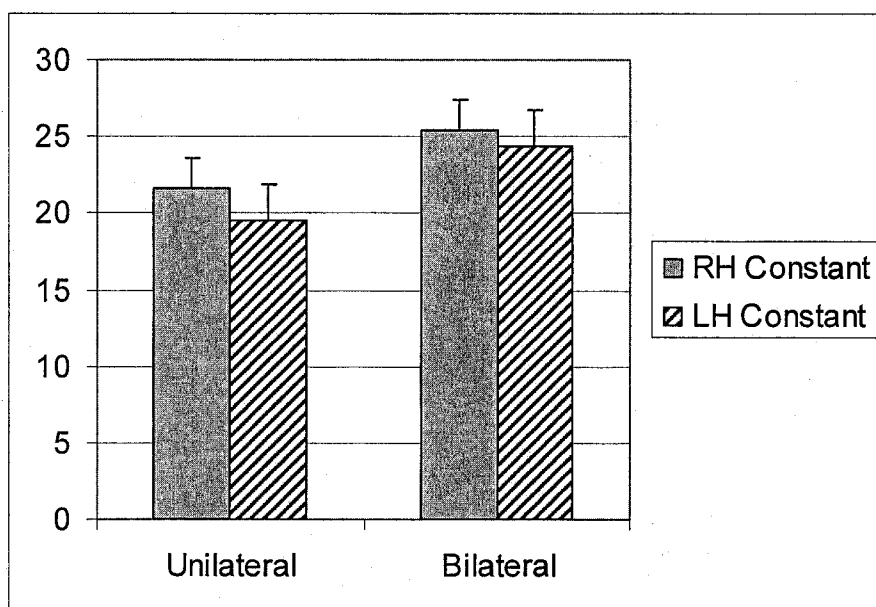


Figure 4. Mean olfactory constants bar graph. Bar graph showing mean and standard error (+1 SE) of olfactory constants across paradigms ($n = 31$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere; LH = left hemisphere.

Integration of visual stimuli did not support a summation model. In fact, most of the significant differences in ratio scaling for visual stimuli occurred within rather than between hemispheres. In general, bilateral visual stimulus presentations (both equal and obscuration) lead to an increase in the size of the exponent and a decrease in the size of the constant over unilateral presentations. Obscuration trials further increased the size of the exponent and decreased the size of the constant in both hemispheres over bilateral stimulation (see Figures 5 and 6). Although a few comparisons did not reach statistical significance, this trend was remarkably consistent across hemispheres and experimental conditions.

Why should bilateral stimulation drive up the size of the exponent and drive down the size of the constant? One explanation may relate to the assertion by Heilman and colleagues (Heilman & Van Den Abell, 1980; Heilman et al., 1987) that novel visual stimuli activate the cerebral hemispheres. Cerebral activation may alter the form of the power function (the size of the exponent and constant) by accelerating the ratio at which perceived stimulus magnitude grows in response to changes in physical magnitude. Because objective magnitude stayed constant across experimental conditions, only perceived intensity was free to change. Obscuration trials may produce even greater changes in the size of the exponent and constant because they are larger stimuli and are presumably more capable of inducing cerebral activation. This conclusion is tentative because it was not predicted before our study, but it raises an interesting and novel possibility that cerebral activation alters ratio scaling by accelerating the growth rate for perceived stimulus intensity.

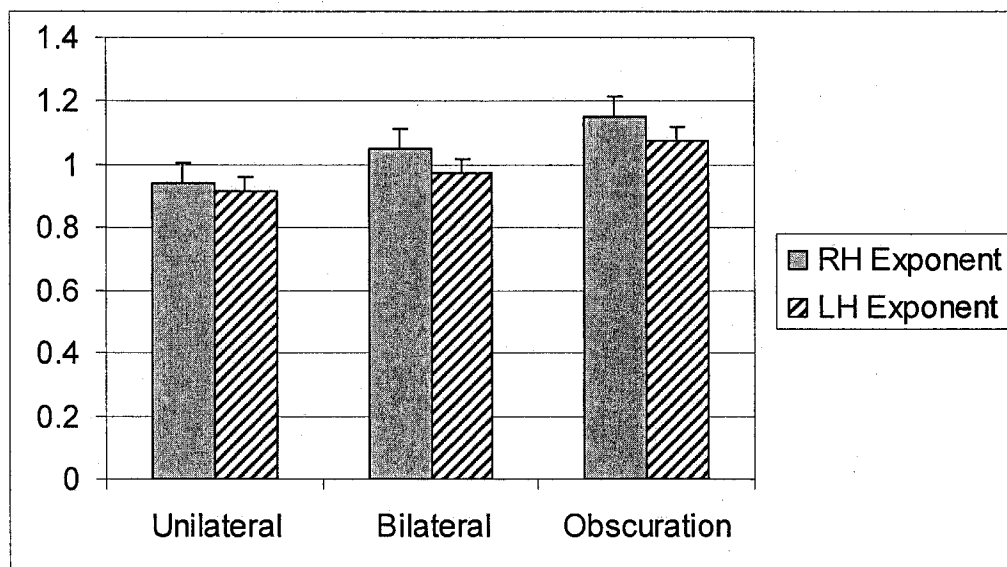


Figure 5. Mean visual exponents bar graph. Bar graph showing mean and standard error (+1 SE) of visual exponents across paradigms ($n = 20$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere; LH = left hemisphere.

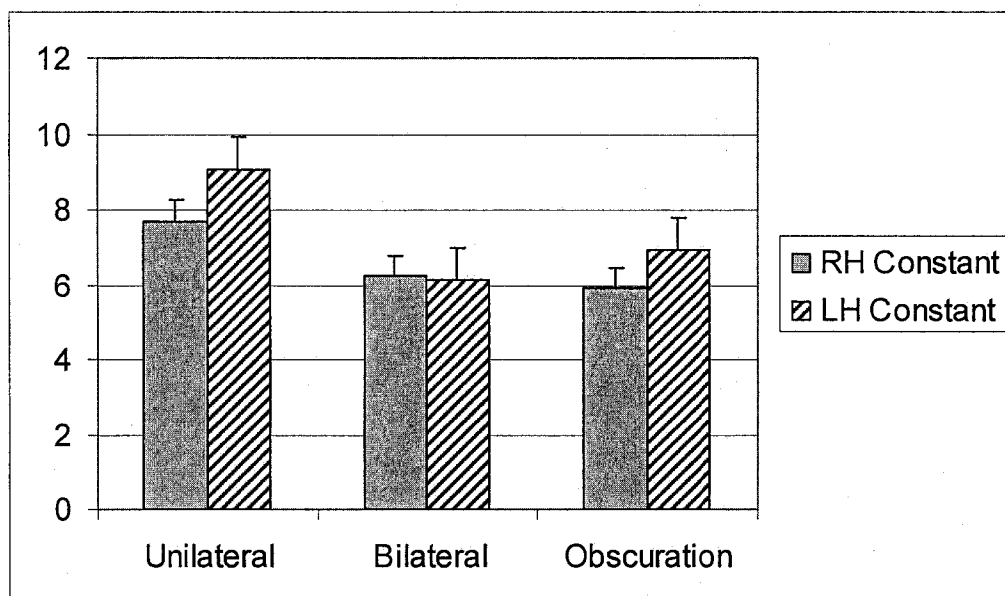


Figure 6. Mean visual constants bar graph. Bar graph showing mean and standard error (+1 SE) of visual constants across paradigms ($n = 20$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere; LH = left hemisphere.

A second general finding is related to variability in ratio scaling. Variability is indexed by the size of the r^2 . Whereas the sizes of the exponent and constant were not correlated with r^2 during equal bilateral visual stimulus presentations, they were significantly correlated with r^2 during unequal stimulus presentations (both unilateral and obscuration) (see Table 2). We refer to these trials as unequal because the magnitude of stimulation delivered to each hemisphere is different in these conditions. Hemispheric competition in the form of unequal stimulation was associated with increased variability (low r^2) in visual ratio scaling (see Figure 7). This finding is similar to that of a neglect case study mentioned earlier (Chatterjee et al., 1998) in which ratio scaling in the damaged hemisphere was obliterated when the non-damaged hemisphere performed the task simultaneously.

It is important to emphasize that the size of the exponent and constant (the form of the power function) maintain a degree of independence from the size of the r^2 (the fit of the power function). Consider, for example, that variability was increased during obscuration trials but that the size of the exponent was highest and the size of the constant was lowest in this condition. Variability is also increased in the unilateral stimulation conditions; however, the exponent is lowest, and the constant is highest. We interpret this to mean that cerebral activation alters the form of the power function and that unequal cerebral activation alters the fit of data to the function.

The same influences appear to be present in studies of ratio scaling after unilateral brain injury. Neglect patients have increased variability, lower exponents, and higher constants than normal subjects and patients without neglect do (Chatterjee, 1995;

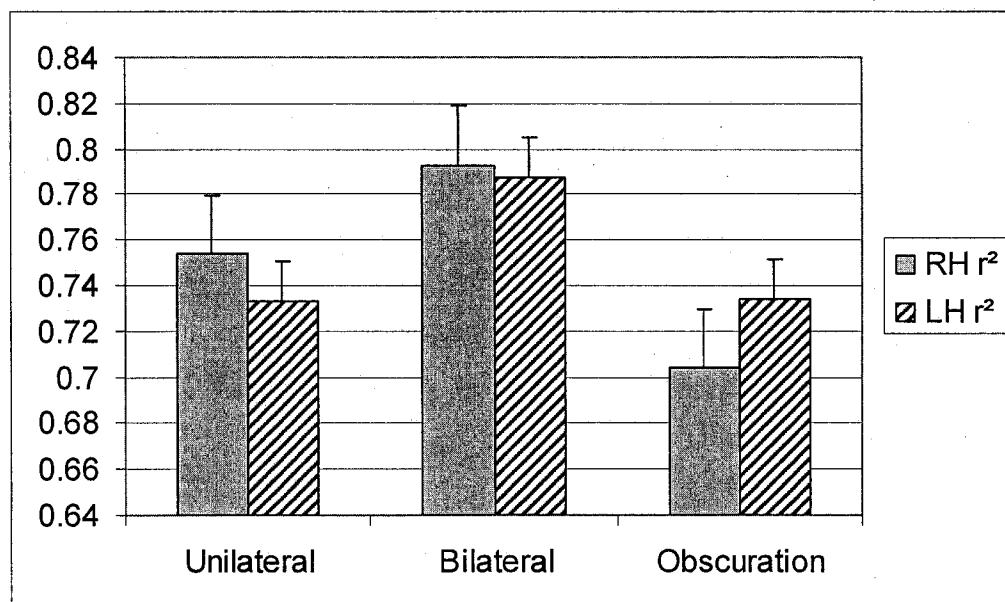


Figure 7. Visual r^2 correlations bar graph. Bar graph showing mean and standard error (+1 SE) of visual r^2 across paradigms ($n = 20$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere, LH = left hemisphere.

Chatterjee, Dajani, & Gage, 1994; Chatterjee, et al., 1992b; Chatterjee, Mennemeier, & Heilman, 1994; Mennemeier et al., 1998, 2002 in press). It may follow that the damaged hemisphere is unable to represent stimuli equal to that of the nondamaged hemisphere. As mentioned earlier, the capacity for cerebral activation is reduced after right-hemisphere injury and particularly in neglect (Coslett et al., 1987). Therefore, novel environmental stimuli may fail to sufficiently activate one or both hemispheres following brain injury, thereby leading to a decreased exponent and increased constant; in addition, the resulting unequal representation alters (increases) the variability. Again, these conclusions are tentative but very intriguing because they suggest that altered ratio scaling in neglect has multiple sources of variance.

We did not examine obscuration trials using olfactory stimuli; as a result we do not know whether increased stimulation would drive up the size of the exponent and drive down the size of the constant, as was the case for visual stimuli. However, comparisons between bilateral and unilateral olfactory stimulation did not support such an outcome. Unlike visual stimuli, bilateral olfactory stimulation led to a fractional increase in perceived intensity rather than a change in ratio scaling. Another difference between visual and olfactory stimuli was that r^2 correlated with the size of the exponent (but not the constant) in both unilateral and bilateral conditions (see Figure. 8). The findings appear to suggest that olfactory stimulation is integrated (summed) between hemispheres, whereas visual stimulation is not.

In conclusion, similarities in the way the two hemispheres construct mental representations of stimulus intensity appear to be greater than differences. Models concerning the integration of ratio scaling between hemispheres, dominance, summation, and inter

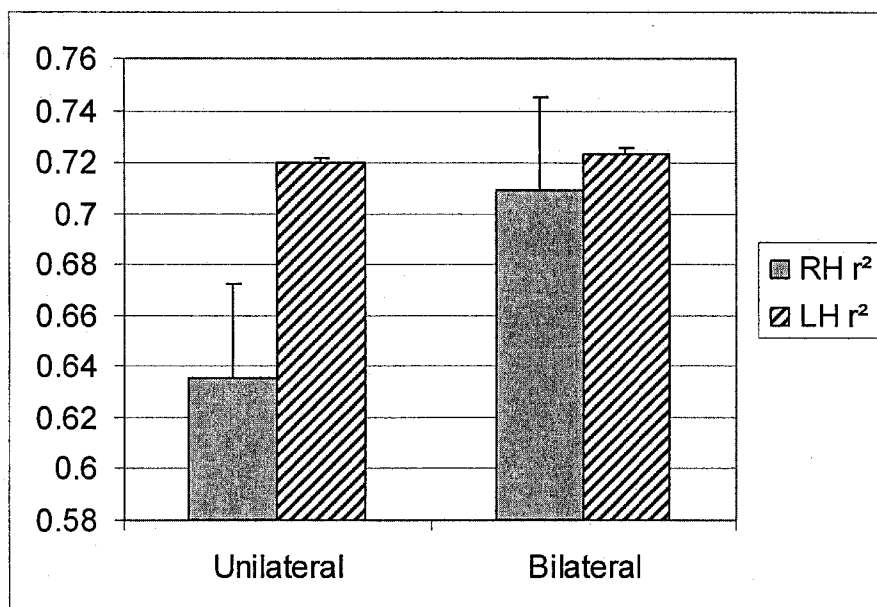


Figure 8. Olfactory r^2 correlations bar graph. Bar graph showing mean and standard error (+1 SE) of olfactory r^2 across paradigms ($n = 20$). Standard error is indicated by lines at the end of each bar. RH = right hemisphere, LH = left hemisphere.

hemispheric inhibition may be modality specific. No model accounted for the integration of visual stimuli between hemispheres, whereas a summation model accounted for olfactory stimuli. The novel and intriguing findings of this study suggest that the form of power functions for visual stimuli are influenced by cerebral activation, whereas the fit of power function is influenced by the equivalency of stimulation (and presumably activation) in each hemisphere.

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APPENDIX A
INFORMED CONSENT FORM

“Contributions of the Left and Right Hemisphere to Ratio Scaling”

Informed Consent

Principal Investigator: Tracy Kretzmer, M.A.

Telephone: (205) 975-8810

Faculty Advisor: James Baños, Ph.D.

Telephone: (205) 934-3454

Sponsor: None

Explanation of Procedures

You are being asked to participate in a research study that investigates how the brain makes judgments about the intensity of smells. If you choose to participate, you will be asked to complete 2 parts of this study. During the first part you will be asked to rate the intensity of smell for 5 concentrations of a non-toxic solution. This smell is not unpleasant to most people. Your ratings will be made by turning a dial with your right or left hand. The smells will be presented to each nostril or both nostrils together. The second part of the study is the same as the first, except you will be using the opposite hand. Your time commitment to participate in this study should not be more than 45 minutes, and you may choose to discontinue at any time.

Potential Risks, Inconveniences and Discomforts

There are very few risks to you as a result of participating in this project. Some people may find the repetitive nature of these tasks to be fatiguing or boring. We will try to avoid this by giving you breaks and allowing you to pace your own performance.

Benefits

The potential benefits of this study include a better understanding of brain function. This information could possibly be used to develop new treatment strategies for patients with strokes or brain injuries who have difficulty interpreting the intensity of some sensory stimuli. It will certainly be of value to scientists who are interested in understanding brain hemisphere differences and how people make size estimates. Participation in this study will not provide direct benefit to you.

Alternative Procedures

Alternatives to obtain extra course credit are available. You may speak with your instructor or Dr. Ed Cook (Undergraduate Subject Pool Coordinator) at (205) 934-3850 to find out more about those options.

Confidentiality

In order to protect your privacy, the information gathered during this study will be kept confidential to the extent permitted by law. Information collected during the study will be kept separately from information that identifies you. The information will be analyzed by Tracy Kretzmer, M.A. Some of the data from your participation may be used in educational presentations and publications, but your name or any other identifying information will never be used.

Participant's Initials _____

The UAB Institutional Review Board for Human Use may review the research records for auditing purposes.

Withdrawal Without Prejudice

You are free to withdraw your consent and to discontinue participation in this project at any time without prejudice or loss of extra course credit.

Significant New Findings

All new findings determined during the course of this research, which may influence your desire to continue your participation, will be provided to you by Tracy Kretzmer or her faculty advisor, Dr. James Baños if such information becomes available.

Cost of Participation

There will be no cost to you for participation in this research.

Payment of Participation in Research

You will not be monetarily paid for participation in this research. One extra credit point will be awarded for each 30 minute segment of research participation as required by UAB Department of Psychology and Dr. Ed Cook, Subject Pool Coordinator (205) 934-3850.

Payment of Research Related Injuries

UAB has made no provision for monetary compensation in the event of injury resulting from the research and in the event of such injury, treatment is provided, but is not provided free of charge.

Questions

If you have any questions about the research or a research related injury, at any time you may contact: Tracy Kretzmer, M.A. (205-975-8810) or her faculty advisor Dr. James Baños (205-934-3454, UAB pager 7799). If you have questions regarding your rights as a research participant, you may contact Ms. Sheila Moore, Director of the Office of the Institutional Review Board for Human Use (IRB). Ms. Moore may be reached at (205) 934-3789 or 1-800-822-8816, press the option for an operator/attendant and ask for extension 4-3789 between the hours of 8 a.m. and 5 p.m. CT, Monday through Friday. If you have questions regarding your participation points for class credit, you may contact Dr. Ed Cook, Subject Pool Coordinator at the UAB Department of Psychology (205) 934-3850.

Legal Rights

You are not waiving any of your legal right by signing this consent form.

Signatures

Your signature below indicates that you agree to participate in this study. You will receive a copy of this signed informed consent.

Signature of Participant or Legally Authorized Representative	Print Name	Date
Signature of Investigator	Print Name	Date
Signature of Witness	Print Name	Date
Signature of person obtaining consent (if other than the investigator)	Print name	Date



Form 4: IRB Approval Form
Identification and Certification of Research
Projects Involving Human Subjects

UAB's Institutional Review Boards for Human Use (IRBs) have an approved Federalwide Assurance with the Office of Human Research Protections (OHRP). The UAB IRBs are also in compliance with 21 CFR Parts 50 and 56 and ICH GCP Guidelines. The Assurance became effective on November 24, 2003 and the approval period is for three years. The Assurance number is FWA00005960.

Principal Investigator: KRETZMER, TRACY S

Co-Investigator(s):

Protocol Number: X050203003

Protocol Title: *Contributions of the Left and Right Hemisphere to Ratio Scaling*

The IRB reviewed and approved the above named project on 03-03-05. The review was conducted in accordance with UAB's Assurance of Compliance approved by the Department of Health and Human Services. This Project will be subject to Annual continuing review as provided in that Assurance.

This project received EXPEDITED review.

IRB Approval Date: 3-3-05

Date IRB Approval Issued: 03-03-05

Marilyn Doss

Marilyn Doss, M.A.
Vice Chair of the Institutional Review
Board for Human Use (IRB)

Investigators please note:

The IRB approved consent form used in the study must contain the IRB approval date and expiration date.

IRB approval is given for one year unless otherwise noted. For projects subject to annual review research activities may not continue past the one year anniversary of the IRB approval date.

Any modifications in the study methodology, protocol and/or consent form must be submitted for review and approval to the IRB prior to implementation.

Adverse Events and/or unanticipated risks to subjects or others at UAB or other participating institutions must be reported promptly to the IRB.

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**GRADUATE SCHOOL
UNIVERSITY OF ALABAMA AT BIRMINGHAM
DISSERTATION APPROVAL FORM
DOCTOR OF PHILOSOPHY**


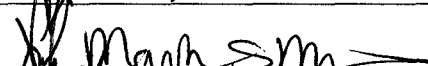
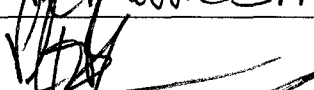


Name of Candidate Tracy Kretzmer


Graduate Program Psychology

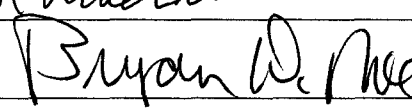
Title of Dissertation Contributions of the Left and Right Hemisphere to
Ratio Scaling

I certify that I have read this document and examined the student regarding its content. In my opinion, this dissertation conforms to acceptable standards of scholarly presentation and is adequate in scope and quality, and the attainments of this student are such that she may be recommended for the degree of Doctor of Philosophy.

Dissertation Committee:

Name	Signature
<u>Scott Richards</u> , Co-Chair	
<u>Mark Mennemeier</u> , Co-Chair	
<u>Paul D. Blanton</u>	
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Director of Graduate Program 

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