

Antonio F. Fortes · Hugo Merchant
Apostolos P. Georgopoulos

Comparative and categorical spatial judgments in the monkey: “high” and “low”

Received: 5 June 2003 / Revised: 3 September 2003 / Accepted: 4 September 2003 / Published online: 7 October 2003
© Springer-Verlag 2003

Abstract Adult human subjects can classify the height of an object as belonging to either of the “high” or “low” categories by utilizing an abstract concept of midline that divides the vertical dimension into two halves. Children lack this abstract concept of midline, do not have a sense that these categories are directional opposites, and their categorical and comparative usages of high(er) or low(er) are restricted to the corresponding poles. We investigated the abilities of a rhesus monkey to perform categorical judgments in space. We were also interested in the presence of the congruity effect (a decrease in response time when the objects compared are closer to the category pole) in the monkey. The presence of this phenomenon in the monkey would allow us to relate the behavior of the animal to the two major competing hypotheses that have been suggested to explain the congruity effect in humans: the analog and semantic models. The monkey was trained in delayed match-to-sample tasks in which it had to categorize objects as belonging to either a high or low category. The monkey was able to generate an abstract notion of midline in a fashion similar to that of adult human subjects. The congruity effect was also present in the monkey. These findings, taken together with the notion that monkeys are not considered to think in propositional terms, may favor an analog comparison model in the monkey.

Keywords Categorization · Spatial cognition · High–low · Rhesus monkey

A. F. Fortes · H. Merchant · A. P. Georgopoulos (✉)
Brain Sciences Center (11B), Veterans Affairs Medical Center,
One Veterans Drive, Minneapolis, MN 55417, USA
Tel.: +1-612-7252282, Fax: +1-612-7252291,
e-mail: omega@umn.edu

A. P. Georgopoulos
Departments of Neuroscience, Neurology,
Psychiatry and Cognitive Sciences Center,
University of Minnesota, Minneapolis, MN 55455, USA

Introduction

Young children (around 3 years of age) seem to interpret dimensional terms dealing with height in a disjoint fashion (Smith et al. 1988). This is to say that they do not have a clear understanding that something that is high is necessarily not low, and something that is low is necessarily not high. For example, when comparing two objects along a dimension, say two objects hanging on a wall, only objects lying close to the floor are considered low and only objects lying close to the ceiling are considered high, with objects in between being classified as neither high nor low. By the age of 5, however, children progress from this notion of disjoint categories to a concept of two categories that share a boundary and have opposing directions (Smith et al. 1988), for example, everything above a certain cut-off line is considered high and everything below it is considered low.

The psychological processes for the representation of terms such as high or low, have been heavily formulated and modeled, and hotly contested, on the basis of language-based, propositional grounds (Banks et al. 1977; Banks and Flora 1977) or on the basis of spatial cognition and “analog arithmetic” (Holyoak 1978; Holyoak and Paterson 1981). Research in the field of comparative judgments has yielded two clear-cut findings. First, the reaction time (RT) decreases as the distance between the two attributes being compared increases, the so-called symbolic distance effect. This means that subjects can compare pairs of remote items faster than pairs of close items. Second, the RT decreases when the form of the comparative judgments matches the position of the target item in the ordering. For example, it is faster to choose the higher of two objects when the pair is placed near the ceiling than when placed near the floor (congruity effect).

The ability of monkeys to categorize objects is well documented. These animals have been trained in a plethora of categorization tasks including: distinguishing between images of cats and dogs (Freedman et al. 2001), parametrized line drawings of fish and faces (Sigala et al. 2002), speed of tactile stimuli (Romo et al. 1993, 1995, 1996,

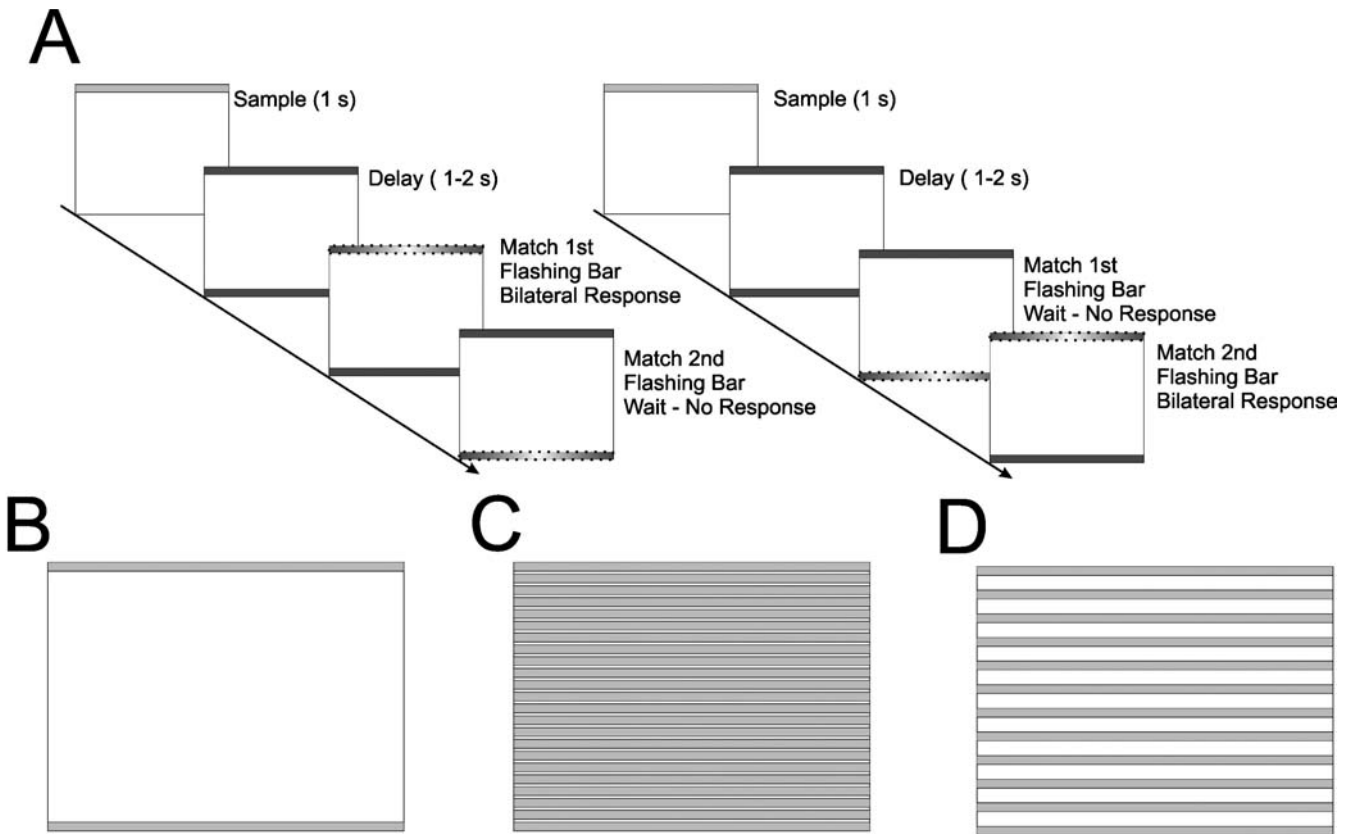


Fig. 1A–D Schematic representation of the delayed match-to-sample task in experiment 1. **A** Delayed match-to-sample task. **B** Position of sample yellow bars used for training the monkey. **C** Position of sample bars used for the probing task. **D** Position of sample bars used during the forced-midline task

1997; Merchant et al. 1997), 3-D computerized animal models (Logothetis et al. 1995; Sugihara et al. 1998) and natural objects such as trees versus non-trees (Vogels 1999a, 1999b; Thomas et al. 2001). Additionally, cortical lesions in monkeys may produce qualitatively similar impairments to those seen following cortical damage in humans (Dias et al. 1996, 1997; Zainos et al. 1997; Vallar et al. 1999; Karnath et al. 2001). Humans and monkeys share homologous cortical areas involved in dealing with space (Bremmer et al. 2001) and it is therefore possible that humans and monkeys share some of the neural substrate and strategies used to deal with space. We trained one monkey in two categorical judgment experiments.

The first question in experiment 1 was to test the ability of the monkey to categorize bars on a monitor as being either high or low in a delayed match-to-sample task. The second question was to observe the monkey's intrinsic categorization scheme and compare it to the behavior of human adults and children. In order to characterize the monkey's behavior we implemented a probing technique in which the monkey was shown special probing trials that were intermixed with normal trials and that appeared randomly only 5% of the time. These trials had different

reward contingencies than normal trials; the animal was rewarded for any response.

As mentioned previously, explanations of the congruity effect differ sharply between propositional and analog hypothesized models. In experiment 2 we tested for the presence of the congruity effect in the monkey and analyzed the behavior with respect to the two classes of models.

Experiment 1

The primary objectives of experiment 1 were to determine whether the monkey behaved similarly to young children or like older children and adults, in the sense of whether it possessed a clear understanding of the directions of difference between the high (H) and low (L) categories, or, if it treated them as disjoint categories not sharing a boundary. If the monkey did possess an intrinsic cut-off line for the two categories, we also wanted to verify whether it was equidistant from the two extreme reference points as is the case with adult human subjects, or whether it was located at a site different from the real midline.

Methods

Animal and apparatus

A male rhesus monkey (*Macaca mulatta*, 6-kg body weight) was used in this study. The monkey was on a regulated

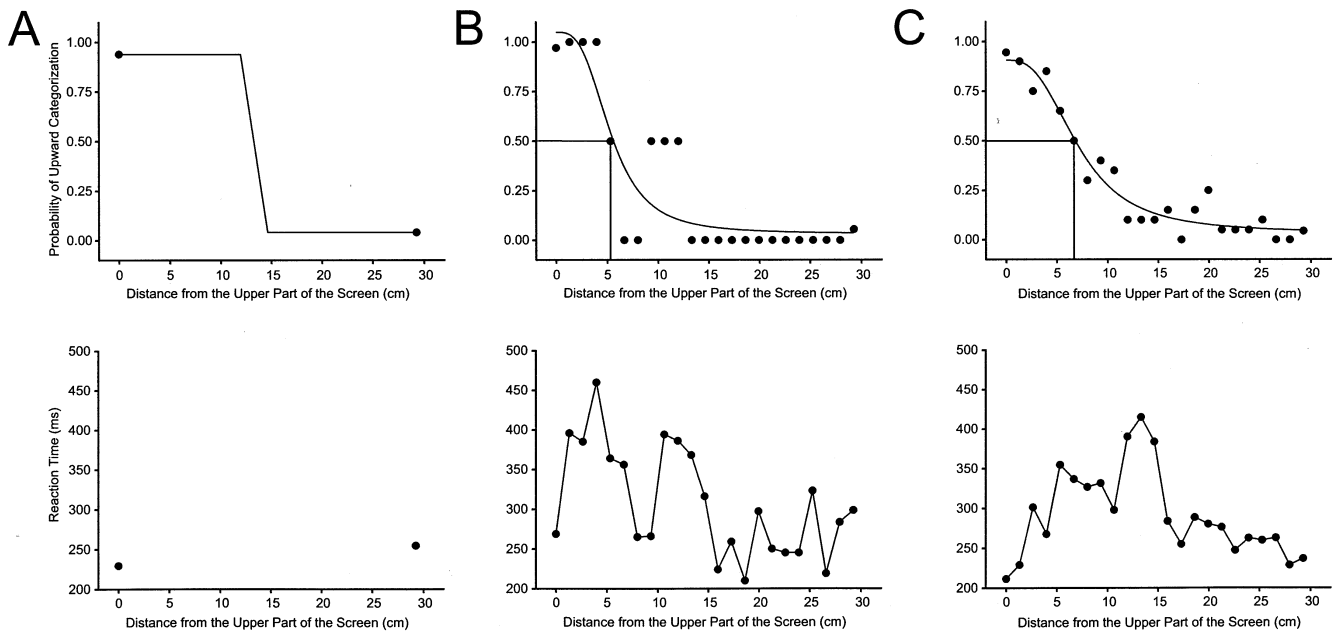


Fig. 2A–C *Top* Behavior of the monkey given by the probability of upward categorization vs the height of the sample yellow bar from the top of the monitor. *Bottom* Reaction times vs the height of the sample yellow bar from the top of the monitor. **A** Response of the monkey 1 day before the commencement of the probing task. **B** Behavior on the first day of probing task. **C** Mean behavior over the 12 probing task sessions

water schedule. The animal protocols were approved by the Institutional Review Board. The monkey sat in a primate chair located 33 cm away from a 30×40 cm computer monitor refreshed at 60 Hz (Vivitron 21, Gateway), both of which were situated inside a sound attenuating room (Vocal Booth). All task-related events were computer controlled. The chair's height was adjusted so that eye-level was situated in the middle of the monitor.

Basic task

The monkey was first trained to categorize bars at the extremes of the monitor as H or L by simultaneously depressing two foot pedals in a delayed match-to-sample task. The sample stimulus consisted of a yellow bar (1.25×40 cm) that could appear in one of two positions on the screen (Fig. 1B) for 1 s. Following the presentation of the yellow bar, two green response bars (of the same size as the sample yellow bar), located at the top and bottom extremes of the monitor appeared during a variable delay period (1–2 s). Then, these bars flashed sequentially for 800 ms each (Fig. 1A) and acted as the “go” signal. The order of flashing was random. In order to obtain a juice reward (0.1 ml drop) the monkey had to depress both push-pedals when the (green) flashing response bar was in the matching position of the sample (yellow) bar. The time window allowed for this response was 150–800 ms after the correct bar started to flash. The monkey was

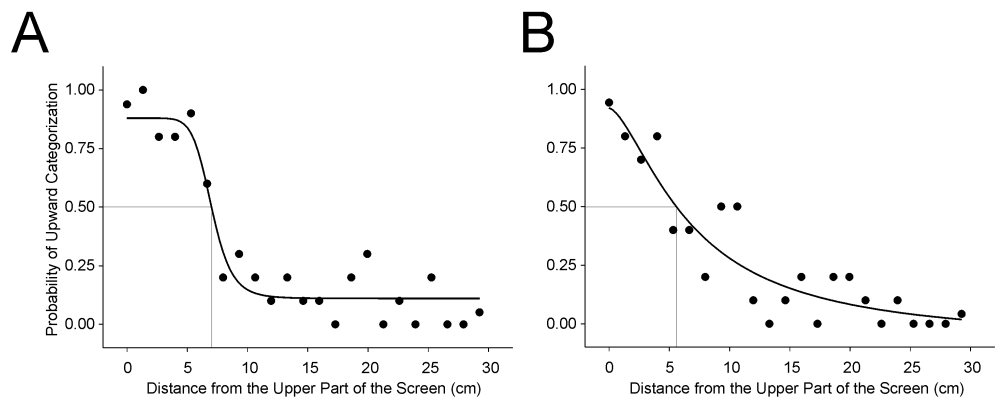
trained for 2–5 h per day approximately five times a week in the delayed match-to-sample task for approximately 1 year. On average 1,000 trials were performed daily.

Probing task

After the monkey was over-trained and performing the previous delayed match-to-sample (DMTS) task at over 95% correct, we probed the monkey's intrinsic cut-off line by displaying the sample yellow bars at positions other than the two extremes of the monitor. There were a total of 21 possible positions: 10 in the lower half of the screen, 1 in the middle of the screen and 10 in the upper half of the screen (Fig. 1C). The sequence of events and the display times were the same as in the basic task.

To determine the intrinsic cut-off line we employed a task that was designed to avoid biasing the monkey into favoring one or the other category response while observing its intrinsic strategy (Church and Deluty 1977). To accomplish this objective we intermingled probing trials (sample yellow bars of intermediate heights, see Fig. 1C) with normal trials (sample yellow bars of extreme heights, see Fig. 1B) in a way that the probing trials would appear randomly at only 5% of the trials. Just as importantly, the reward contingency for the probing trials was also different: the monkey always received a reward. This is to say that the monkey received a reward for any response in the task, including trials with no responses at all. The no-response behavior would be analogous to the behavior of young children with a disjoint notion of the categories. In this way the reward outcome of previous responses would not bias the response in subsequent probing trials. Training sessions containing intermediate-height trials occurred once or twice a week for a total of 12 sessions.

Fig. 3A, B Behavior of the monkey given by the probability of upward categorization vs the height of the sample yellow bar from the top of the monitor, when the matching response bar was the first to flash (**A**), and when the matching response bar was the second to flash (**B**)



Forced midline task

Following the 12 probing sessions we changed the reward contingency so that the cut-off line was imposed and placed in the middle of the screen. The monkey received a reward only when matching stimuli above the cut-off line to the H bar or below the midline to the L bar. The stimuli used to change the monkey's intrinsic cut-off line to a true midline are shown in Fig. 1D. The sequence of events and the display times were the same as in the basic task. All positions of the sample bar were equally probable.

Data analysis

Sigmoidal functions were calculated using a logistic regression in order to determine the cut-off line for the H and L categories. These curves were plotted as the probability of matching the stimulus as H against the distance of the bar from the top of the screen (Fig. 2). The logistic regression is given by:

$$p = \frac{(p_1 - p_4)}{1 + \left(\frac{h}{p_3}\right)^{p_2}} + p_4,$$

where p_1 and p_4 correspond to the minimum and maximum values of the proportion of responses matching to H, p_2 is the estimated slope and p_3 corresponds to the value of h (the distance from the top of the screen) at half of the maximum value of p . This regression was carried out in Axum (v 5, MathSoft, Cambridge, Mass., 1996).

It is important to mention that this study is based on the behavior of one animal, which raises concerns about the generalization of the results obtained. However, two factors need to be taken into consideration. First, the monkey was trained and studied for more than 1 year in which we collected thousands of trials. The performance of the animal during this period was consistent with the results shown here. Second, preliminary data from a second monkey is in full agreement with the results reported. Therefore, the present results may reflect the behavior of these animals in general.

Results and discussion

Figure 2A shows that the monkey's behavior on the day prior to commencing the probing trials was greater than 95% correct. On the first day of probing the monkey responded to all intermediate height probing trials. The boundary between the two categories was not at the true midline – but was biased upwards, at 5.6 cm away from the top of the screen (Fig. 2B). Given that the total distance from the top and bottom was 30 cm, this bias was approximately one fifth of the way nearer the top. Over the 12 probing sessions the mean cut-off line using the modeled sigmoidal fit was located at 6.8 cm away from the top, approximately one quarter of the way between the top and bottom of the screen (Fig. 2C). The bottom of Fig. 2 shows that the RT of the monkey was higher for the probing trials than for the training set, indicating that the monkey was not guessing, but rather performed a mental calculation for the categorical judgment. In addition, the RT increased at the screen position where higher indecision was observed. Finally, it is important to mention that the monkey responded in all the trials, independently of where the sample bar was located, which contrasts with the lack of responses to intermediate positions in children (Smith et al. 1986, 1988).

Figure 3 shows the sigmoidal functions for responses when the matching bar was the first to flash (Fig. 3A) and when the matching bar was the second to flash (Fig. 3B). The cut-off line was 7 and 5.6 cm, respectively.

In summary, the monkey was able to classify bars both at the extremes as well as in intermediate heights as belonging to either the H or L categories. In this sense it behaved like human adults and older children, which indicates that it may possess an “either-or” notion as opposed to a “disjoint” category concept (Smith et al. 1988). Nonetheless, the animal did not separate the two categories into equal halves of the screen, and in this respect behaved differently from humans. In a similar task, namely a bisection point task where the duration between two stimuli is categorized, it has been shown that the cut-off value separating “long” and “short” categories corresponds to the geometric mean of the extreme values in rats (Church and Deluty 1977). In humans this value is equal to the arithmetic mean (Wearden et al. 1997). Averaging

Fig. 4A, B *Top* Behavior of the monkey given by the probability of upward categorization vs the height of the sample yellow bar from the top of the monitor. *Bottom* Reaction times vs the height of the sample yellow bar from the top of the monitor. **A** Response during 5 representative days. **B** Mean response for these 5 days. After the change in reward contingency the new abstract midline of the animal was located in the center of the screen (threshold: 15 cm from the top)

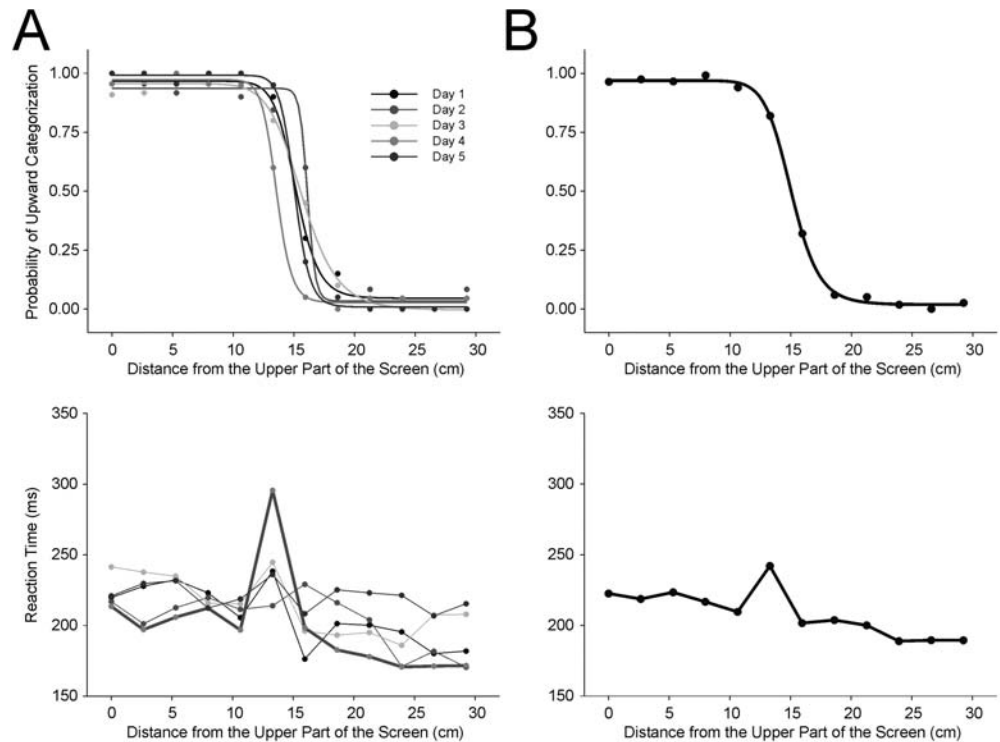
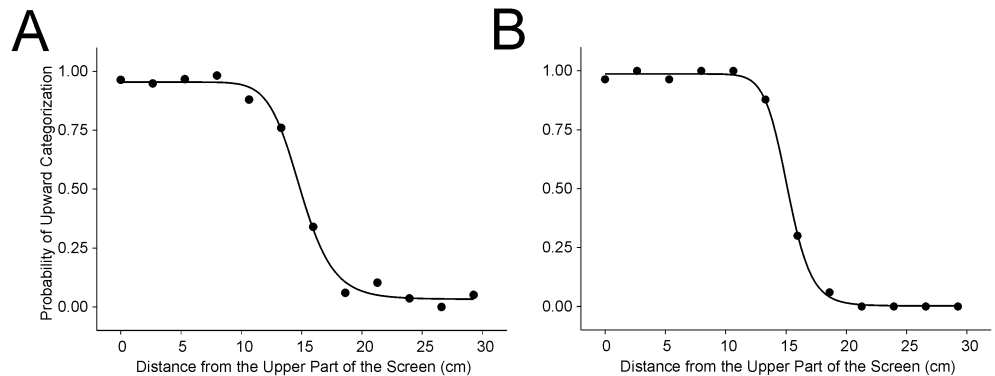


Fig. 5A, B The probability of upward categorization is plotted against the height of the sample bar. **A** Psychometric performance of the monkey in the psychometric task when the matching bar was the first to flash (threshold: 14.9 cm from the top). **B** Performance of the monkey in the psychometric task when the matching bar was the second to flash (threshold: 15.1 cm from the top)



has been shown to occur in humans and pigeons in the spatial and temporal dimensions simultaneously in similar probing tasks (Cheng et al. 1996).

Once the reward contingency changed so that the monkey had to match all stimuli above the real midline as H and below it as L, we were able to shift the monkey's intrinsic cut-off line to a true midline between the two categories. Figure 4A shows data for five representative days with the new reward contingency. During these days the performance of the monkey was above 85% of correct trials. Figure 4B shows the mean response for the 5 days of this training. The monkey changed the psychometric cut-off line to the true midline located at 15 cm. The response for when the matching bar was the first to flash and when the matching bar was the second to flash can be seen in Fig. 5. There was no significant difference between the two. The thresholds for match first and match second are 14.9 cm and 15.1 cm, respectively. The RTs were higher, again, at the screen locations that were close to the cut off

line. In summary, the probing of the monkey's response to previously untrained stimuli revealed that the animal was able to create an abstract cut-off line and to categorize a continuous variable, in this case vertical space.

Experiment 2

When the form of the comparative judgments matches the position of the target item in the ordering, the RT for the comparison decreases. This phenomenon is termed the congruity effect. Two major classes of models have been proposed for the congruity effect: the semantic coding model (Banks and Flora 1977) and analog reference point model (Holyoak 1978). The first class assumes that discrete tags represent information. For example, large objects will be tagged as L and their relative sizes can be further differentiated by recoding them into L and L+ (Banks

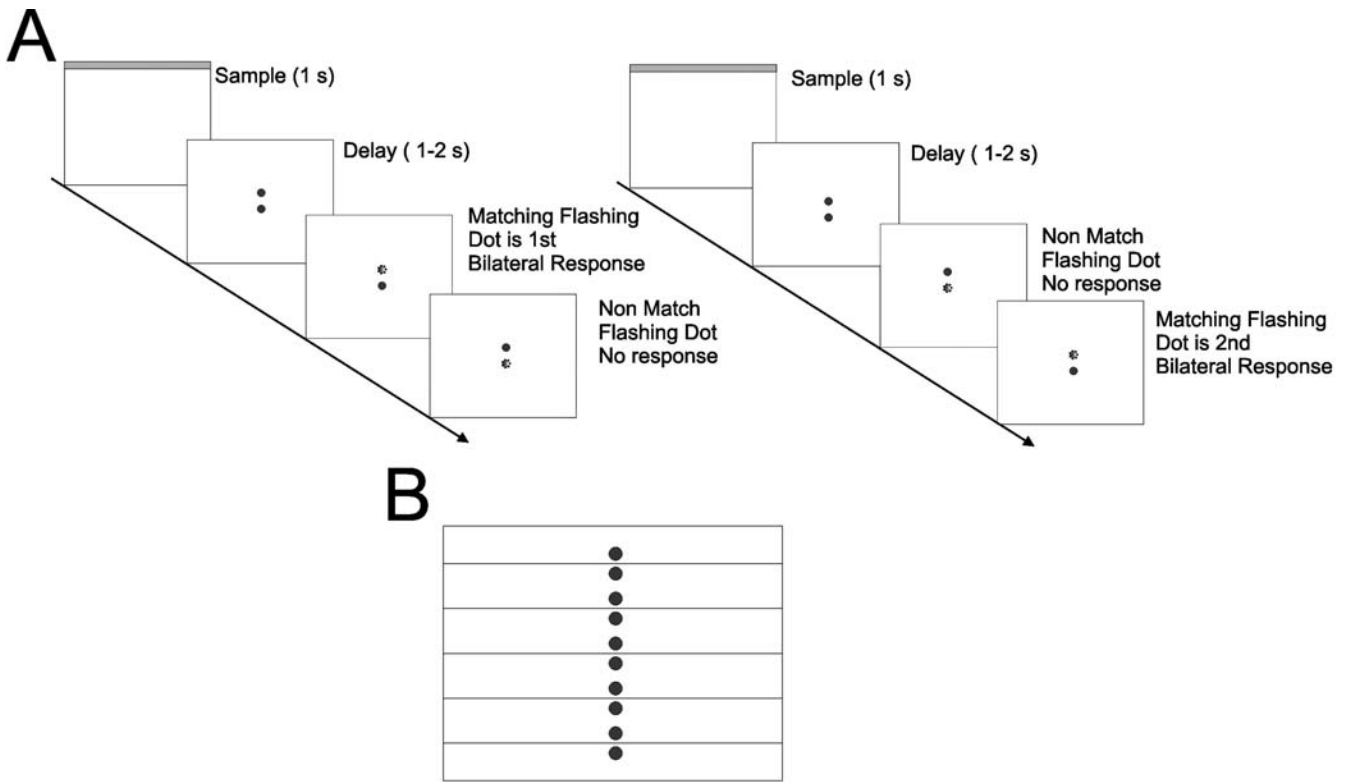


Fig. 6A, B Schematic representation of the delayed match-to-sample task used in experiment 2. **A** Match-to-sample task. **B** Position of the green response circle pair used

and Flora 1977). The same reasoning follows for the objects of small size. The congruity effect is then due to two things. First, when the form of the question matches the tag for the object this object is immediately chosen. Second, when the tag does not match the form of the question the objects must be recoded and this additional time taken to recode would be responsible for the increase in the RT.

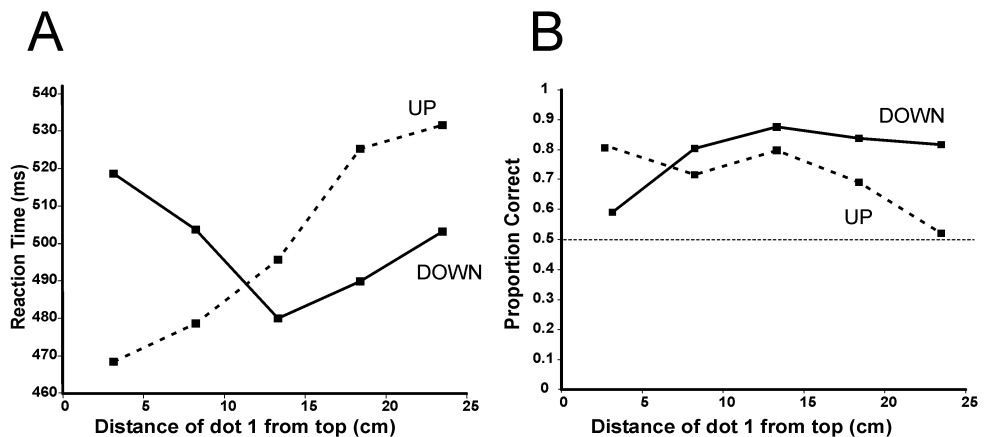
The second class of models assumes two reference points: one for large and one for small. These reference points can be set at the end of the distribution. The object's mental distance from the reference point is then calculated. The reference point chosen to calculate the dis-

tance depends on the form of the question (Holyoak 1978). If the object's representation is far from the reference point it is being compared to, the RT will increase, accounting for the congruity effect. The main objective of experiment 2 was to test for the presence of the congruity effect in the monkey.

Methods

The sample stimulus consisted of a horizontal yellow bar (1.25×40 cm) that could appear in one of two positions on the screen, either at the top or bottom, for 1 s. Following the presentation of the sample yellow bar, two green response circles with a fixed distance of 3.8 cm appeared for a variable delay period (1–2 s) in one of five positions on

Fig. 7A, B Congruity effect in the monkey. **A** RT (ms) vs the distance of the upper response circle from the top of the screen. **B** Percentage of correct (when the correct match was to the first flashing circle) vs the distance of the upper response circle from the top of the screen. Dot 1 is the uppermost circle in the circle pair



the screen (Fig. 6) and flashed sequentially for 1 s each. The position of the circle pair and the order in which the circles flashed was random within the set. In order to obtain a correct trial and receive a juice reward, the monkey had to depress the push-pedals when the green flashing response circle was in the corresponding category of the sample yellow bar previously presented; for example, the top circle if the yellow bar was presented at the top of the screen or the bottom circle if the bar was presented at the bottom. The time window allowed for this response was 150–800 ms after the proper circle started to flash.

Initial training was carried out using only the intermediate position of the response circle pair and lasted approximately 6 weeks. Only after the monkey's performance was >90% correct did we display the five circle positions. Initially the monkey had problems responding to the circle pair when it was located in the bottom half of the screen; additional training with the circle pair only in the lowest positions was carried out for 3 days prior to data collection.

Results and discussion

In general, the monkey showed a higher ability to match the H sample bar to the top-flashing circle when this was closer to the top of the screen and vice-versa for the L sample bar. The monkey had a higher percentage correct at the middle of the screen, which may be due to a training effect (Fig. 7A). The RTs followed the pattern stipulated by the congruity effect: When the top-flashing circle was closer to the top of the screen RTs were shorter for matching it to the H sample bar than when it was closer to the bottom of the screen.

Monkeys are not considered to think in propositional terms (Sanders 1985). Here, the comparison task does not involve a verbal command, and taken together these lead us to favor the analog reference point model over the semantic congruence model in monkeys and suggests that the same kind of strategy may be used in humans.

General discussion

The monkey's categorical usage was not limited to the extremes of the monitor, as we would expect for 3-year-old children. Rather the monkey was able to draw a cut-off line to distinguish between the two categories much like adult human subjects would. The cut-off line was not at the middle however, being biased towards the downward part of the screen. It is noteworthy that the monkey possessed an understanding that intermediate height objects belonged to one of the two category groups, suggesting that it may hold an understanding that high and low have opposite directions of difference.

The two heavily disputed models for the congruity effect, (1) propositional or language-based (Banks et al. 1977; Banks and Flora 1977) and (2) "analog arithmetic" are more easily tested in monkeys since they do not have

an explicit language and are not thought to think in propositional terms (Sanders 1985). The presence of the congruity effect in the monkey favors an analog model, suggesting that humans also use this method to perform comparative judgments.

Another interesting case concerns mental rotation. This task is commonly thought to involve an analog rotation process (Shepard and Cooper 1982) although explanations based on a propositional model have also been offered (Pylyshyn 1981). Neural data recorded during mental rotation of an intended movement direction (Georgopoulos and Massey 1987; Georgopoulos et al. 1989), revealed an analog process of rotation from a reference direction. Altogether, these findings support the notion of analog processing of spatial cognitive information in both human subjects and monkeys.

Acknowledgements This work was supported by United States Public Health Service grant NS17413, the United States Department of Veterans Affairs, and the American Legion Brain Sciences Chair. Animal care conformed to the principles outlined in *The Guide for Care and Use of Laboratory Animals* (National Institutes for Health publication no. 85–23, revised 1985).

References

- Banks WP, Flora J (1977) Semantic and perceptual processes in symbolic comparisons. *J Exp Psychol Hum Percept Perform* 3:278–290
- Banks WP, Clark HH, Lucy P (1977) The locus of the semantic congruity effect in comparative judgements. *J Exp Psychol Hum Percept Perform* 1:35–47
- Bremner F, Schlack A, Duhamel JR, Graf W, Fink GR (2001) Space coding in primate posterior parietal cortex. *Neuroimage* 14:S46–51
- Cheng K, Spetch ML, Miceli P (1996) Averaging temporal duration and spatial position. *J Exp Psychol Anim Behav Process* 22:175–182
- Church RM, Deluty MZ (1977) Bisection of temporal intervals. *J Exp Psychol Anim Behav Process* 3:216–228
- Dias R, Robbins TW, Roberts AC (1996) Primate analogue of the Wisconsin Card Sorting Test: effects of excitotoxic lesions of the prefrontal cortex in the marmoset. *Behav Neurosci* 110:872–886
- Dias R, Robbins TW, Roberts AC (1997) Dissociable forms of inhibitory control within prefrontal cortex with an analog of the Wisconsin Card Sort Test: restriction to novel situations and independence from "on-line" processing. *J Neurosci* 17:9285–9297
- Freedman DJ, Riesenhuber M, Poggio T, Miller EK (2001) Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* 291:312–316
- Georgopoulos AP, Massey JT (1987) Cognitive spatial-motor processes. 1. The making of movements at various angles from a stimulus direction. *Exp Brain Res* 65:361–370
- Georgopoulos AP, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. *Science* 243:234–236
- Holyoak KJ (1978) Comparative judgements with numerical reference points. *Cogn Psychol* 10:203–243
- Holyoak KJ, Patterson KK (1981) A positional discriminability model of linear-order judgments. *J Exp Psychol Hum Percept Perform* 7:1283–1302
- Karnath HO, Ferber S, Himmelbach M (2001) Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* 411:950–953

- Logothetis NK, Pauls J, Poggio T (1995) Shape representation in the inferior temporal cortex of monkeys. *Curr Biol* 5:552–563
- Merchant H, Zainos A, Hernandez A, Salinas E, Romo R (1997) Functional properties of primate putamen neurons during the categorization of tactile stimuli. *J Neurophysiol* 77:1132–1154
- Pylyshyn ZW (1981) The imagery debate: analogue media versus tacit knowledge. *Psychol Rev* 88:16–45
- Romo R, Ruiz S, Crespo P, Zainos A, Merchant H (1993) Representation of tactile signals in primate supplementary motor area. *J Neurophysiol* 70:2690–2694
- Romo R, Merchant H, Ruiz S, Crespo P, Zainos A (1995) Neuronal activity of primate putamen during categorical perception of somesthetic stimuli. *Neuroreport* 6:1013–1017
- Romo R, Merchant H, Zainos A, Hernandez A (1996) Categorization of somesthetic stimuli: sensorimotor performance and neuronal activity in primary somatic sensory cortex of awake monkeys. *Neuroreport* 7:1273–1279
- Romo R, Merchant H, Zainos A, Hernandez A (1997) Categorical perception of somesthetic stimuli: psychophysical measurements correlated with neuronal events in primate medial premotor cortex. *Cereb Cortex* 7:317–326
- Sanders RJ (1985) Teaching apes to ape language: explaining the imitative and nonimitative signing of a chimpanzee (*Pan troglodytes*). *J Comp Psychol* 99:197–210
- Shepard RN, Cooper L (1982) *Mental images and their transformations*. MIT Press, Cambridge, Mass.
- Sigala N, Gabbiani F, Logothetis NK (2002) Visual categorization and object representation in monkeys and humans. *J Cogn Neurosci* 14:187–198
- Smith LB, Cooney NJ, McCord C (1986) What is “high”? The development of reference points for “high” and “low”. *Child Dev* 57:583–602
- Smith LB, Rattermann MJ, Sera M (1988) “Higher” and “lower”: comparative and categorical Interpretations by Children. *Cogn Dev* 3:341–357
- Sugihara T, Edelman S, Tanaka K (1998) Representation of objective similarity among three-dimensional shapes in the monkey. *Biol Cybern* 78:1–7
- Thomas E, Van Hulle MM, Vogels R (2001) Encoding of categories by noncategory-specific neurons in the inferior temporal cortex. *J Cogn Neurosci* 13:190–200
- Vallar G, Lobel E, Galati G, Berthoz A, Pizzamiglio L, Le Bihan D (1999) A fronto-parietal system for computing the egocentric spatial frame of reference in humans. *Exp Brain Res* 124:281–286
- Vogels R (1999a) Categorization of complex visual images by rhesus monkeys. Part 1. Behavioural study. *Eur J Neurosci* 11:1223–1238
- Vogels R (1999b) Categorization of complex visual images by rhesus monkeys. Part 2. Single-cell study. *Eur J Neurosci* 11:1239–1255
- Wearden JH, Rogers P, Thomas R (1997) Temporal bisection in humans with longer stimulus durations. *Q J Exp Psychol B* 50:79–94
- Zainos A, Merchant H, Hernandez A, Salinas E, Romo R (1997) Role of primary somatic sensory cortex in the categorization of tactile stimuli: effects of lesions. *Exp Brain Res* 115:357–360