Anim Cogn (2011) 14:535–544
DOI 10.1007/s10071-011-0388-3

ORIGINAL PAPER

Endogenous-like orienting of visual attention in rats

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Received: 31 August 2010 / Revised: 8 February 2011 / Accepted: 14 February 2011 / Published online: 3 March 2011

Abstract This study investigated the orienting of visual attention in rats using a 3-hole nose-poke task analogous to Posner, Information processing in cognition: the Loyola Symposium, Erlbaum, Hillsdale, (1980) covert attention task for humans. The effects of non-predictive (50% valid and 50% invalid) and predictive (80% valid and 20% invalid) peripheral visual cues on reaction times and response accuracy to a target stimulus, using Stimuli-Onset Asynchronies (SOAs) varying between 200 and 1,200 ms, were investigated. The results showed shorter reaction times in valid trials relative to invalid trials for both subjects trained in the non-predictive and predictive conditions, particularly when the SOAs were 200 and 400 ms. However, the magnitude of this validity effect was significantly greater for subjects exposed to predictive cues, when the SOA was 800 ms. Subjects exposed to invalid predictive cues exhibited an increase in omission errors relative to subjects exposed to invalid non-predictive cues. In contrast, valid cues reduced the proportion of omission errors for subjects trained in the predictive condition relative to subjects trained in the non-predictive condition. These results are congruent with those usually reported for humans and indicate that, in addition to the exogenous capture of attention promoted by both predictive and non-predictive peripheral cues, rats exposed to predictive cues engaged an additional slower process equivalent to human's endogenous orienting of attention. To our knowledge, this is the first demonstration of an endogenous-like process of covert orienting of visual attention in rats.

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Keywords Rat · Covert orienting · Attention · Endogenous attention · Reaction time

Introduction

In the covert attention paradigm (Posner 1980), human subjects gazing at a central fixation point are exposed to a signaling cue and then have to press a key when they detect a visual target presented to the right or left. The cue may include either an arbitrary symbol (*central cues*), presented close to the fixation point, indicating to where the subject has to orient attention covertly or a peripheral stimulus presented close to the target location (*peripheral cues*). In addition, the cue may indicate the target location correctly (valid cue) or incorrectly (invalid cue) and be predictive (80% valid and 20% invalid) or non-predictive (50% valid and 50% invalid).

Shorter reaction times (RT) in valid when compared to invalid trials (validity effect) are revealed for certain combinations of variables including Stimulus-Onset Asynchrony (SOA), cue type (peripheral or central), and cue predictability, suggesting that different processes underlie orienting of attention (see Luck and Vecera 2002, for review). For example, while *predictive central* cues produce validity effects beginning at SOAs between 100 and 200 ms, reaching a plateau at 300 ms and maintained for at least 500 ms, *non-predictive central* cues do not produce any validity effects (Berger et al. 2005; Jonides 1981; Müller and Findlay 1988; Müller and Rabbitt 1989). This validity effect, induced by predictive central cues, is ascribed to the time taken for decoding and interpreting the central cue and for orientation of endogenous attention. In contrast, *non-predictive peripheral* cues generate validity effects starting for SOAs around 50 ms, reaching a peak between 100 and

150 ms; in this case, the validity effect is ascribed to the exogenous capture of attention (Azevedo et al. 2001; Bartolomeo et al. 2007; Berger et al. 2005; Posner et al. 1978; Posner and Cohen 1984; Wright and Richard 2000); further SOA increments lead to an inversion of the validity effect, named inhibition of return, with a peak between 300 and 400 ms. *Predictive peripheral* cues also generate validity effects starting for SOAs around 50 ms reaching a peak at about 100–150 ms; similarly, this validity effect is also ascribed to the capture of exogenous attention. However, in contrast to non-predictive peripheral cues, the validity effect generated by predictive peripheral cues is maintained for longer SOAs, indicating that predictability of the cue stimulates later engagement of endogenous attention which is then capable of overcoming the inhibition of return effect (Bartolomeo et al. 2007; Berger et al. 2005; Müller and Findlay 1988; Posner and Cohen 1984; Wright and Richard 2000).

This pattern of results has stimulated the notion that processing of visual stimuli is influenced by exogenous and endogenous orienting of attention (Berger et al. 2005; Corbetta and Shulman 2002; Folk et al. 1992; Jonides 1981; Juola et al. 2000; Luck and Vecera 2002; Müller and Rabbitt 1989; Warner et al. 1990). The exogenous orienting of attention, similar to that seen when using *non-predictive* peripheral cues, would engage a stimulus-related bottom-up automatic capture of attention. In contrast, the endogenous orienting of attention, like that seen when using *predictive* symbolic (or central) cues, would depend on the subjects' top-down expectancies about the impending stimulus, which is believed to be related to "conscious effortful" processes, volition, or intention (Jonides 1981; McCormick 1997; Müller and Findlay 1988; Müller and Humphreys 1991; Posner and Snyder 1975). Note that *predictive* peripheral cues would lead to engagement of both exogenous and endogenous attention; however, their time courses would be different, i.e., faster for exogenous attention and slower for endogenous attention (see Luck and Vecera 2002, for review).

In the covert attention task involving human beings, the eyes are maintained on fixed area. Therefore, the same sensory information during target presentation is provided in valid and invalid trials. Similarly, the same motor response is required in valid and invalid trials. Therefore, one cannot ascribe the effects of valid and invalid cues to intrinsically tied sensory or motor mechanisms. The difference between reaction times in invalid and valid trials, the validity effect for reaction times, reflects both the benefit achieved by the prior orienting of attention toward the expected target location and the costs of prior orienting of attention toward an incorrect target location that thus required the inhibition of this attentional focus and the re-orienting of attention to detect the target presented at another location (Posner 1980).

There have been demonstrations that rats exposed to analogous tasks using peripheral cues exhibit SOA-dependent validity effects that are ascribed to exogenous (automatic) orienting of attention (e.g., Rosner and Mittleman 1996; Phillips and Brown 2000; Ward and Brown 1996; Ward et al. 1998; Weese et al. 1999). We carried out a careful comparison of the results of these studies and observed that while *non-predictive* peripheral cues induced a validity effect restricted to SOA of 200 ms but not longer SOAs (Weese et al. 1999), *predictive* peripheral cues induced validity effects for both short and longer SOAs, i.e., between 200 and 400 ms (Ward and Brown 1996); 5, 15, and 55 centiseconds (Rosner and Mittleman 1996); and 200, 400, and 800 ms (Ward et al. 1998).

Our hypothesis for this pattern of results is that when exposed to *non-predictive* peripheral cues, rats engage exogenous attention, as proposed by Rosner and Mittleman (1996), Ward and Brown (1996), Ward et al. (1998), and Weese et al. (1999), whereas when exposed to *predictive* peripheral cues, both exogenous and endogenous attention are engaged. Exogenous attention generates validity effects at short SOAs only, and endogenous attention generates validity effects at longer SOAs, as proposed in human studies (see above).

Note that prior studies evaluated groups subjected to either predictive or non-predictive cues, but did not include two independent groups of subjects, one exposed to predictive and the other to non-predictive cues subjected to similar procedures within the same study, and thus to comparable experimental conditions; this latter approach would have allowed statistical evaluation of potential SOA-related differences in validity effects. However, that pattern of results arose from different studies, employing distinct behavioral procedures, and thus could be ascribed to either experimental or procedural differences instead of representing an actual phenomenon.

The aim of this study was to evaluate the hypothesis that exposure to *predictive* peripheral cues render rats capable of orienting both exogenous attention at short SOAs and endogenous attention at longer SOAs, thus replicating, for the first time, the pattern of results usually seen for human beings exposed to analogous procedures (see above). In addition to the conceptual importance of revealing processes of endogenous orienting of attention in rats, if confirmed, this would open novel possibilities of using this animal model in studies on the neurobiology of attention. The effects of non-predictive (50% valid and 50% invalid) and predictive (80% valid and 20% invalid) peripheral visual cues on response accuracy and reaction times (RT) to a target stimulus with SOAs varying between 200 and 1,200 ms were investigated in independent groups of subjects, exposed to comparable experimental procedures. Peripheral cues were expected to capture exogenous atten-

tion for both subjects exposed to predictive cues and subjects exposed to non-predictive cues; therefore, one should observe validity effects at shorter SOAs for both groups. Furthermore, subjects exposed to predictive peripheral cues were expected to orient endogenous attention in addition to exogenous attention; thus, one should observe validity effects also at longer SOAs. Differently, subjects exposed to non-predictive peripheral cues were not expected to orient endogenous attention; therefore, one should observe validity effects restricted to shorter SOAs.

Materials and methods

Animals

Eleven naïve, 3- to 4-month-old male Wistar rats were used. The subjects were individually housed in standard rat laboratory cages. Light was provided from 07:00 to 19:00 h, and room temperature was maintained at 22 ± 3°C. A food restriction schedule started 1 week before the beginning of training and was maintained until the end of the experiment. The rats had free access to food for a time period of 3 h, starting 15 min after the end of each daily behavioral session; during the remaining time, no food was available in the cages. Behavioral procedures were conducted between 09:00 and 13:00 h. These housing conditions lasted until the end of the experiments.

All procedures and animal care complied with the guidelines from the Laboratory for Neuroscience and Behavior of the Biosciences Institute at the University of São Paulo, which conforms to national and international standards and policies.

Apparatus

Three identical white operant chambers, measuring $26 \times 26 \times 26$ cm, were used. One of the walls contained three horizontally adjacent recessed holes, each measuring 2.5 cm square and 4.5 cm in length, located at the center of the wall, 7.5 cm from the chamber floor. These holes could individually provide different levels of illumination (dim lights corresponded to 50 Lux and bright lights corresponded to 250 Lux, both measured at the entrance of the hole) for brief durations under computer control by a bulb recessed in the rear end of the hole. At the central portion of each hole, 0.5 cm from the entrance, there was a photocell connected to a computer that recorded breaks in a vertically mounted infrared beam whenever the rat's nose poked into the hole. A drinking device located 5.7 cm beneath the center hole and aligned with its center on a 5-cm-wide horizontal platform protruding from the wall dispensed 20 μl of a 10% sucrose solution used as a reward under computer control. The chamber was illuminated by a house light located in the center of the ceiling. A micro-camera positioned at the ceiling of the chamber allowed for the monitoring of animal behavior within the apparatus. Each operant chamber was located within a sound-attenuating box with a fan that generated a low level of white noise and promoted air renovation within the operant chamber. The complete system was monitored by a computer-controlled clock calibrated to provide millisecond precision for measurements and to control events (prior tests using an oscilloscope confirmed this level of temporal precision).

Procedure

At the beginning of each experimental session, the house light was on.

Conditioning

During the conditioning phase, the lateral holes were sealed with white plastic covers. Each rat was individually trained to insert its nose in the center hole whenever its bright light was on. This nose-poke and consequent interruption of the infrared beam immediately switched the hole's light off. The initial time period required for the rat to maintain its nose within the hole was 100 ms, and the fulfillment of this requirement led to a reward. If the rat failed to do so, all lights, including the chamber light, were switched off for a "time-out" period lasting 4,000 ms. As conditioning proceeded, the nose-poke time period required was gradually increased; 20 consecutive correct responses led to an increase of 50 ms while 5 consecutive incorrect responses led to a 50-ms decrease. Completion of this phase was reached when the rat was capable of maintaining its nose within the center hole for at least 1,000 ms. Each session lasted either 30 min or 500 trials, whichever happened first.

Pre-training

During the pre-training phase, all three holes were available. The subjects were trained to nose-poke into the center hole, at which time its bright light was extinguished, then to nose-poke the lateral hole illuminated with bright light for the duration of 500 ms at early sessions that progressed to 100 ms during later pre-training sessions. This response led to a reward. When the rat either (1) failed to respond to the illuminated lateral hole up to 500 ms by maintaining its nose within the center hole (omission error), (2) withdraw the nose from the center hole either before or within the first 100 ms after the stimulus onset (anticipation error), or (3) inserted its nose within the non-illuminated opposite lateral hole (commission error), no reward was offered, and there was a time-out period. Other types of errors were also

measured including lack of nose-poke into the center hole within the initial 1,000 ms of the beginning of the trial and nose-poke into the lateral holes at the beginning of the trial without prior nose-poke into the center hole; however, they were not included in the analysis because they are relatively rare and provide no meaningful information about attentional processes. The initial time interval between the center hole nose-poke and the presentation of the bright light in one of the lateral holes was 200 ms. As the animal learned the task, this time interval was increased in steps of 50 ms at every 10 consecutive correct responses. A 150-ms duration dim light (the cue) was introduced immediately after the center nose-poke, before presentation of the bright light either in the same or in the opposite lateral hole, depending on the group (see below). When the subject was capable of maintaining its nose within the center hole for at least 1,200 ms after the cue onset, the training phase was initiated. The target stimulus was equally likely to be presented in the left or right lateral holes during all experiments.

According to Weese et al. (1999)

> the eyes of a rat are lateral in its head and thus both cannot be directed to one side only. Exploratory eye movements are thought to be unlikely in the rat … but, rather, orienting head movements are made toward stimuli of interest. Therefore, for confirmation of covert orienting of attention in the rat, it is most important that the head of the rat is maintained centrally and still. The configuration of the poke holes is such that, when the rat makes a sustained nose-poke, its head is oriented forward and level. Any processing enhancement of the target conferred by a peripheral cue cannot therefore be attributable to previous foveation of (i.e., an overt orientation to) the target location but must be caused by a shift in attention. (p. 10,136).

Training

The training phase introduced variable time intervals between the cue and the target. The SOAs used were 200, 400, 800, and 1,200 ms. For six animals, the cue was non-predictive, that is, it appeared randomly on the same side as that of the subsequent target in 50% of trials ("valid" trials) and in the opposite side as that of the subsequent target in the remaining 50% of trials ("invalid" trials). For another 5 animals, the cue appeared on the same side as that of the subsequent target in 100% of trials. Therefore, in this condition, the cue was predictive. Each daily session consisted of 500 trials equally distributed among SOAs and side of the target. Training proceeded until the animal achieved a criterion of 70% correct responses.

To enhance the importance of the visual cues, the target stimulus duration was then decreased along successive training sessions to find the minimal target duration that allowed for the maintenance of the established criterion of correct responses for each subject. This individual target duration, which varied between 50 and 100 ms depending on the subject, was subsequently used for all training and testing sessions.

Testing

Testing sessions were similar to the training sessions. However, while the rats trained in the predictive condition were exposed to 80% of valid trials and 20% of invalid trials in each SOA (Predictive Group), the rats trained in the non-predictive condition were maintained with 50% valid and 50% invalid trials in each SOA (Non-Predictive Group). For both groups, the sequence of trials was random. The reaction time corresponded to the time interval between the target light onset and the nose withdrawal from the center hole. Therefore, a single unique response, nose withdrawal, was employed to measure reaction time in both valid and invalid trials. The movement time corresponded to the time interval between the nose withdrawal from the center hole and its insertion within one of the lateral holes.

To maintain optimal effectiveness of the cues for subjects exposed to the predictive condition, testing sessions were intercalated with training sessions. This alternated sequence was repeated such that the final results correspond to a mean of 10 sessions.

Data analysis

The percentage of correct responses relative to the total number of trials in each condition, considering SOA (200, 400, 800, and 1,200 ms), cue validity (valid and invalid), and cue predictability [predictive (Predictive Group) and non-predictive (Non-Predictive Group)], were obtained for each session. The scores from testing sessions were used for the calculation of the percentage of correct responses in invalid trials minus the percentage of correct responses in valid trials for each condition, thus expressing the "validity effect for response accuracy" (note that negative results in this score reflect that response accuracy in invalid trials was smaller compared with the response accuracy in valid trials). In addition, median reaction times and median movement times for trials with correct responses considering cue validity and SOA were obtained for each session for each rat. Validity effects for reaction times, corresponding to the individual median reaction time in invalid trials minus median reaction time in valid trials as a function of SOA, for subjects exposed to predictive and non-predictive peripheral cues were also calculated. Similarly, the percentage of errors of anticipation, omission, and commission in each condition relative to the total number of trials in each

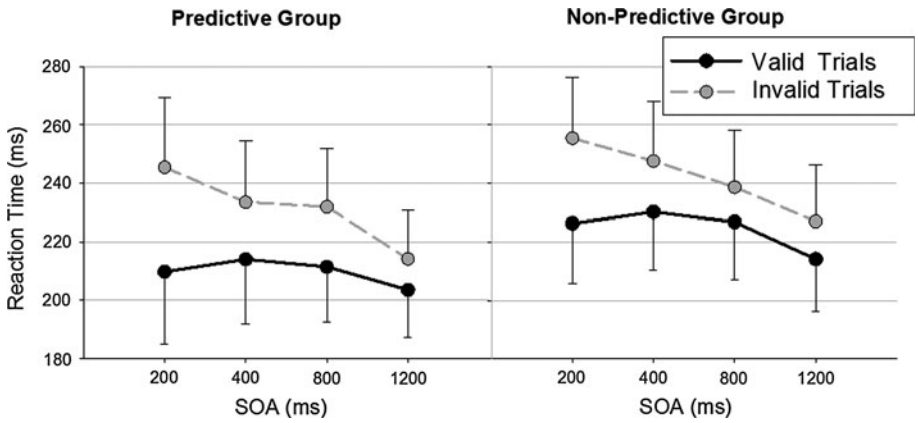

Fig. 1 Mean reaction times (±S.E.M.) as a function of cue validity and SOA in testing sessions for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues

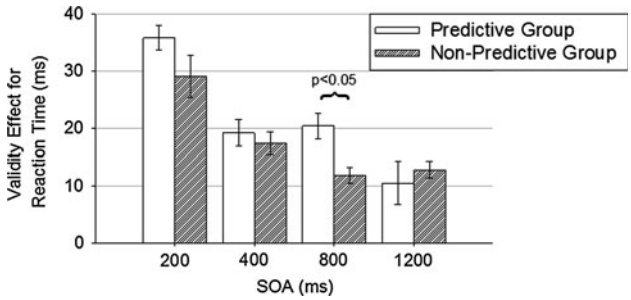

Fig. 2 Validity effect for reaction time (median reaction time in invalid trials minus median reaction time in valid trials ±S.E.M.) as a function of SOAs in testing sessions for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues

condition were individually extracted for each session. These scores were then averaged over the 10 testing sessions, and the resulting individual means were subjected to repeated measures analyses of variance (ANOVA) having Groups (Predictive or Non-Predictive) as the between-subjects factor and Validity and SOA as the within-subjects factors. An independent ANOVA was run for each different parameter using SAS/STAT Software. *Post hoc* analyses, when required, involved an analysis of variance of contrast variables and Duncan's test.

Results

Reaction time

Mean reaction times as a function of cue validity and SOA for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues are presented in Fig. 1. Validity effects for reaction times (median reaction time in invalid trials minus median reaction time in valid trials) as a function of SOA for subjects exposed to predictive and non-predictive peripheral cues are presented in Fig. 2.

ANOVA revealed significant Validity ($F_{1,9} = 202.24$, $P < 0.0001$) and SOA ($F_{3,27} = 6.62$, $P < 0.01$) main effects but a lack of a significant Group main effect ($F_{1,9} = 0.21$, $P = 0.66$). In fact, as illustrated by Figs. 1 and 2, reaction times in valid trials were smaller compared with reaction times in invalid trials for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues. In addition, Fig. 1 shows that as the SOA increased, the reaction times decreased.

ANOVA also revealed significant Validity × SOA ($F_{3,27} = 46.0$, $P < 0.0001$) and Validity × SOA × Group ($F_{3,27} = 3.36$, $P = 0.033$) interaction effects, indicating that the magnitude of the validity effect on reaction times depended on the SOA and on cue predictability. Interestingly, greater validity effects between invalid and valid scores were seen for subjects exposed to predictive cues (Predictive Group) compared with subjects exposed to non-predictive cues when the SOA was 800 ms ($P < 0.05$, Duncan's test) (Fig. 2).

Together, these results indicate that both predictive and non-predictive peripheral cues stimulate a prompt exogenous capture of attention toward the cued location thus reducing reaction times in valid trials compared with invalid trials. In addition, this significantly greater validity effect for subjects exposed to predictive peripheral cues, when compared to subjects exposed to non-predictive peripheral cues when the SOA was 800 ms (Fig. 2), indicates that predictive cues trigger an additional and distinct mechanism that takes longer to be engaged thus increasing the validity effect.

Response accuracy

The mean percentage of correct responses as a function of cue validity and SOA for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues are presented in Fig. 3. The validity effects for response accuracy, i.e., the percentage of correct responses in invalid trials minus the percentage of correct

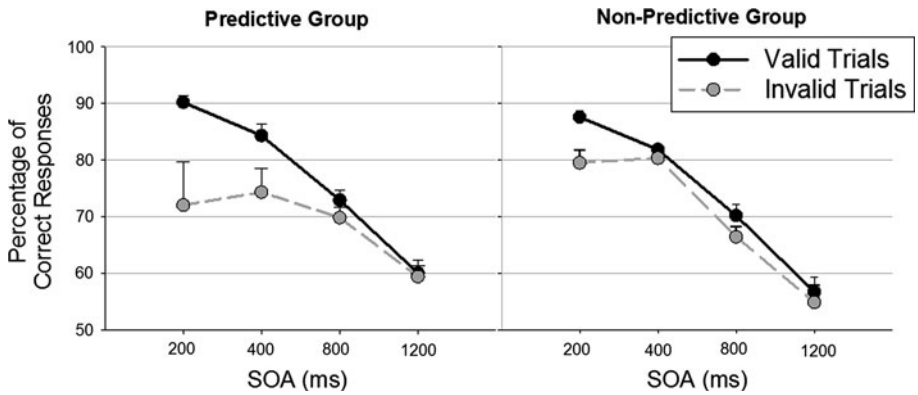

Fig. 3 Mean percentage of correct responses (+S.E.M.) as a function of cue validity and SOA in testing sessions for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues

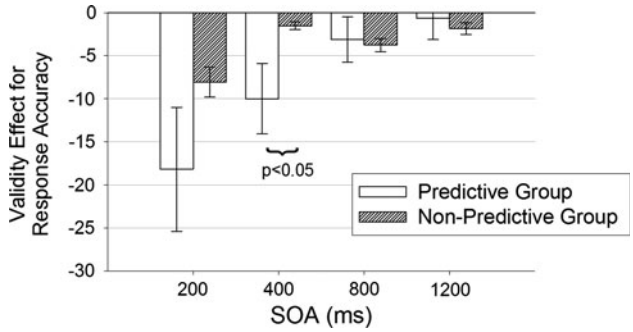

Fig. 4 The validity effect for response accuracy (percentage of correct responses in invalid trials minus the percentage of correct responses in valid trials ±S.E.M.) as a function of SOAs in testing sessions for subjects exposed to predictive (Predictive Group) and non-predictive (Non-Predictive Group) peripheral cues. *Note* that negative results reflect that performance in invalid trials was poorer when compared with performance in valid trials

responses in valid trials for each condition, are presented in Fig. 4.

The ANOVA revealed significant Validity ($F_{1,9} = 11.59$, $P = 0.0078$) and SOA ($F_{3,27} = 65.64$, $P < 0.0001$) main effects but no significant Group main effect ($F_{1,9} = 0.02$, $P = 0.90$). In addition, ANOVA revealed significant Validity × SOA ($F_{3,27} = 13.35$, $P < 0.0005$) and Validity × SOA × Group ($F_{3,27} = 4.42$, $P = 0.03$) interaction effects. As Fig. 3 shows, the percentage of correct responses tended to decrease as the SOA increased. However, subjects exposed to predictive cues exhibited a greater disruption of performance in invalid relative to valid cues, particularly when the SOA was 400 ms, compared with subjects exposed to non-predictive cues ($P < 0.05$, Duncan's test) (Figs. 3, 4).

The percentage of anticipation, omission, and commission errors as a function of cue validity and SOA for subjects exposed to predictive and non-predictive peripheral cues are presented in Fig. 5.

Regarding anticipation errors (Fig. 5a, b), ANOVA revealed a significant SOA main effect ($F_{3,27} = 215.38$, $P < 0.0001$). As expected, the percentage of anticipation errors increased as the SOA increased. ANOVA also revealed significant Validity × Group ($F_{1,9} = 10.47$, $P = 0.02$) and Validity × SOA × Group ($F_{3,27} = 6.82$, $P < 0.05$) interaction effects. Inspection of Fig. 5a and b suggests that the percentage of anticipation errors was slightly greater for subjects exposed to non-predictive cues compared with subjects exposed to predictive cues. In addition, for these latter subjects, the percentage of errors in invalid trials seemed slightly smaller when compared with those seen for valid trials. Note, however, that anticipation errors occurred before the subject was actually exposed to the target stimulus. Thus, one cannot ascribe its occurrence to any within-trial validity condition. The origin of these differences is not clear.

Regarding omission errors (Fig. 5c, d), ANOVA revealed significant Validity ($F_{1,9} = 12.71$, $P = 0.007$) and SOA ($F_{3,27} = 16.73$, $P < 0.001$) main effects, but a lack of a significant Group main effect ($F_{1,9} = 0.49$, $P = 0.50$). In addition, ANOVA revealed Validity × SOA ($F_{3,27} = 12.35$, $P = 0.003$) and Validity × SOA × Group ($F_{3,27} = 3.27$, $P < 0.05$) interaction effects. Although subjects exposed to non-predictive (Fig. 5d) and predictive cues (Fig. 5c) exhibited a greater percentage of omission errors when receiving invalid cues at shorter SOAs, this effect was much stronger for subjects exposed to predictive cues. In fact, a comparison of Fig. 5c and d reveals that subjects exposed to predictive cues exhibited both a reduction in the percentage of omission errors when receiving valid trials and an increase in the percentage of omission errors when receiving invalid trials. These results indicate that, in addition to the automatic capture of attention promoted by peripheral cues, subjects exposed to predictive cues exhibited another process of attention orienting that adds to the first one.

The percentage of commission errors was substantially smaller relative to the other types of errors (Fig. 5e, f). Although ANOVA revealed significant Validity ($F_{1,9} = 20.22$, $P = 0.002$) and SOA ($F_{3,27} = 9.56$, $P = 0.0006$) main effects and a Validity × SOA interaction effect ($F_{3,27} = 15.63$, $P < 0.0001$), a lack of a Group main effect ($F_{1,9} = 0.82$, $P = 0.35$) and Validity × Group ($F_{3,27} = 3.16$, $P = 0.10$), SOA × Group ($F_{3,27} = 0.40$, $P = 0.75$) and

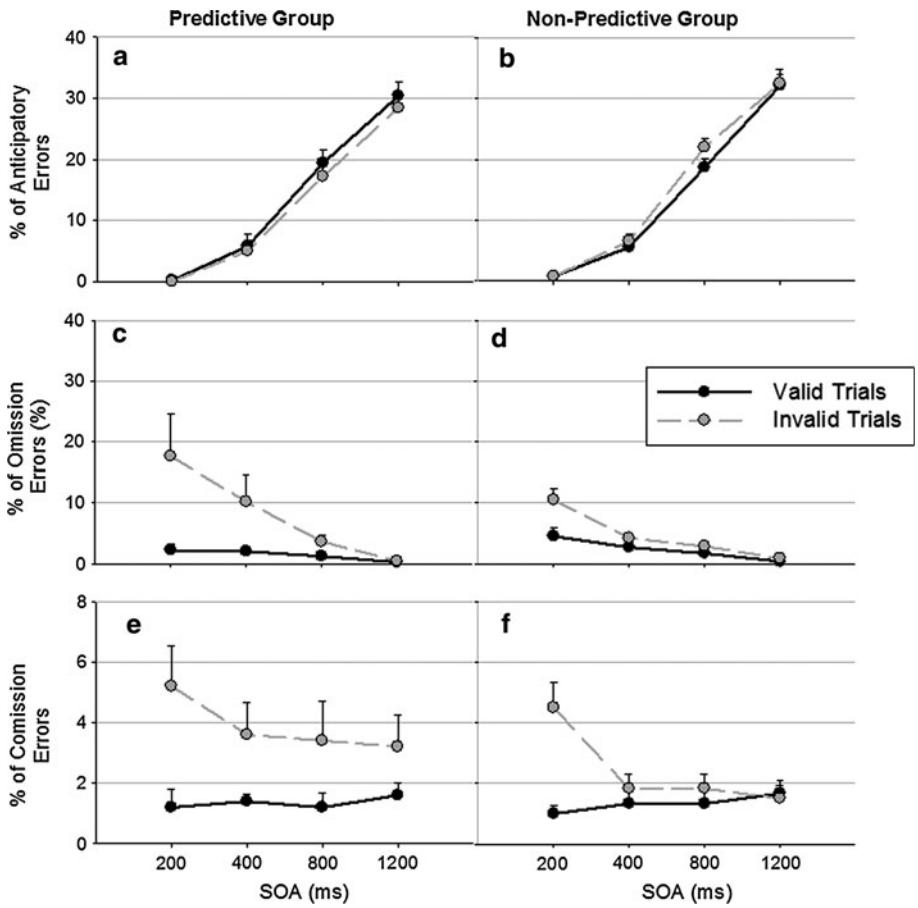

Fig. 5 Mean percentage (+S.E.M.) of anticipation (**a**, **b**), omission (**c**, **d**), and commission (**e**, **f**) errors relative to the total number of trials in each condition as a function of cue validity and SOA in testing sessions for subjects exposed to predictive (Predictive Group) (**a**, **c** and **e**) and non-predictive (Non-Predictive Group) (**b**, **d,** and **f**) peripheral cues. *Note* the scale differences

Validity × SOA × Group ($F_{3,27} = 0.82$, $P = 0.49$) interaction effects was found. Thus, invalid cues increased commission errors, particularly at the shortest SOA. These effects seem to be independent of exposure to predictive or non-predictive cues (Fig. 5e, f).

Movement time

The mean movement times for correct responses were calculated as a function of cue validity and SOA for subjects exposed to predictive (Predictive Group) and non-predictive (Non-predictive Group) peripheral cues (data not presented). The ANOVA revealed a significant Validity main effect ($F_{1,9} = 1.54$, $P = 0.0021$) and significant Validity × SOA ($F_{3,27} = 3.77$, $P = 0.022$) interaction effects, but no significant Group effect ($F_{1,9} = 1.54$, $P = 0.25$).

Discussion

The experimental design used in the present experiments allowed a direct comparison between subjects exposed to predictive or to non-predictive peripheral cues. The results showed that rats tested in a situation analogous to the human's covert attention task exhibited shorter reaction times when predictive and non-predictive peripheral visual cues validly indicated the location of an impending visual target when compared to reaction times when cues invalidly indicated that location (Figs. 1, 2). These results confirm prior findings by Rosner and Mittleman (1996), Ward and Brown (1996; 1997), Ward et al. (1998), and Weese et al. (1999) that valid peripheral cues capture visual attention and facilitate the detection of a visual target stimulus. In addition, our results showed that when the SOAs were 200 and 400 ms, the magnitude of the validity effect for reaction time for subjects exposed to non-predictive (Non-Predictive Group) and predictive (Predictive Group) cues did not differ significantly (Fig. 2), indicating that these validity effects were mainly related to the exogenous capture of attention for both groups. Differently, however, the validity effect for reaction time at SOA 800 ms was significantly greater for subjects trained with predictive cues compared with subjects trained with non-predictive cues (Fig. 2). This effect is associated with a relative increase in reaction time for invalid cues (Fig. 1). Together, these results indicate that in addition to the exogenous capture of attention promoted by peripheral cues that is detectable by way of reaction times at short SOAs, subjects exposed to predictive peripheral cues also engaged another attentional process detectable by way of reaction times at longer

SOAs, equivalent to human's endogenous orienting of attention.

Symbolic predictive cues induce a relatively slow expression of validity effects in humans that is usually ascribed to the time taken for decoding and interpreting the cue and the subsequent orienting of endogenous attention toward the cued location (e.g., Berger et al. 2005; Jonides 1981; Müller and Findlay 1988; Müller and Rabbitt 1989). In contrast, peripheral predictive cues induce both a fast and a slow expression of validity effects in humans; while the fast expression of validity effects is ascribed to exogenous bottom-up capture of attention, the slow expression of validity effects is ascribed to endogenous top-down attention orienting (see Luck and Vecera 2002, for review).

It could be argued that the effects observed in the present study are related to the use of peripheral cues, independently on their predictability. Note, however, that even though both subjects trained with predictive cues and subjects trained with non-predictive cues were exposed to peripheral cues, these effects were observed only for subjects exposed to predictive cues. Therefore, predictive peripheral cues seem to trigger some distinct mechanism detectable by way of reaction times only at longer SOAs.

It could also be argued that peripheral cues that are conditioned to predict the location of the target exert more potent and longer-lasting effects on target detection. However, if this hypothesis was correct, then one should observe more potent and longer-lasting effects on target detection for subjects exposed to the predictive peripheral cues relative to those exposed to the non-predictive peripheral cues, in every SOA tested and not effects restricted to only some longer SOAs. The results clearly showed that the major differences in validity effects for reaction time for subjects exposed to the predictive when compared to the non-predictive peripheral cues were restricted to the SOA 800 ms for reaction times. These figures suggest that a distinct mechanism, that takes time to be engaged, is responsible for this validity effect.

Data involving response accuracy confirm and extend this interpretation. The percentage of correct responses was smaller for subjects exposed to predictive invalid cues relative to subjects exposed to non-predictive invalid cues, particularly at shorter SOAs (Figs. 3, 4). Additional analyses revealed that this smaller accuracy was mainly related to an increase in omission errors (Fig. 5c, d). Congruently, predictive valid cues decreased the amount of omission errors relative to non-predictive valid cues (Fig. 5c, d). In other words, when the cue is predictive and invalid, detection of the target decreases, and when the cue is predictive and valid, detection of the target increases, in contrast to non-predictive cues (Fig. 5c, d). Similar results were observed in relation to commission errors (Fig. 5e, f).

Note that the target duration used in the present experiments was slightly above threshold level and that the time interval available for reaction after target presentation was restricted, thus increasing the attentional demand for task performance. Therefore, the orienting of attention toward the invalidly cued location, as it might occur for subjects trained in the predictive condition, decreased the target detection and increased the amount of omission errors relative to subjects trained in the non-predictive condition (Fig. 5c, d). Together, these results lend further support to the hypothesis that in addition to an exogenous capture of attention, subjects exposed to predictive cues get the benefit of an endogenous attentional process.

Prior studies on both overt attention in rats (Bushnell 1995) and covert attention involving peripheral cues both in monkeys (Bowman et al. 1993) and rats (Phillips et al. 2000; Rosner and Mittleman 1996; Ward and Brown 1996; Weese et al. 1999) have shown greater validity effects for shorter SOAs (when the cue and target stimuli do not overlap), suggesting the engagement of exogenous (automatic) orienting of attention. Jonides (1980; 1981; 1983) investigated the distinction between voluntary and automatic attention in human beings by comparing the effects of cues that either predicted or did not predict the target location. His basic assumption was that predictive cues would allow voluntary shifts of attention to the cued location, thus improving target detection. Because both the cue and target stimuli used were the same in both conditions and in the required response, differences in performance in predictive and non-predictive conditions could be ascribed to the processes engaged in each condition. The present study employed a similar rationale and revealed that rats exhibited a pattern of results compatible with those seen for humans. That is, in addition to the automatic (or exogenous) capture of attention by peripheral cues, rats exposed to predictive cues seem to have engaged processes equivalent to a human's voluntary orienting of attention, also named endogenous attention.

To our knowledge, this is the first study reporting solid evidence supporting the existence of an endogenous process of the covert orienting of visual attention in rats.

The present study also revealed intriguing results. As seen above, for subjects exposed to the predictive condition, invalid cues induced a significantly greater number of omission errors when the SOAs were 200 and 400 ms (Fig. 5c, d). In parallel, these subjects exhibited a greater validity effect for reaction times when the SOA was 800 ms (Fig. 2) associated with a lack of significant differences in the percentage of omission errors (Fig. 5c, d). It is not clear to what extent these results reflect the occurrence of distinct effects of exogenous and endogenous orienting of attention on reaction times and accuracy, or whether they reflect

distinct effects of endogenous orienting of attention on either perceptual or decisional processes.

Prinzmetal et al. (2005) proposed that there are two different mechanisms for the orienting of attention induced by peripheral cues in human beings: (1) an involuntary, reflexive orienting response, for spatial cues even when they do not predict the likely target location, that affects the decision relative to which location to react to ("channel selection"), thus interfering with reaction time but not with response accuracy and (2) a voluntary mechanism driven toward the likely target location that would enhance stimulus perception at that location relative to other locations ("channel or signal enhancement") and thus increase response accuracy and reduce reaction times. Despite the tasks and species differences, the results of the present study may be conceptually interpreted following these guidelines. Our data suggest that exogenous capture of attention occurs for both subjects exposed to predictive and subjects exposed to non-predictive peripheral cues, thus reducing reaction times in valid when compared with invalid trials. This effect would predominate at shorter SOAs, possibly because of its reflexive nature. For subjects exposed to predictive cues, this process would occur in parallel to an endogenous process of attention orienting that extends the validity effects for reaction times to longer SOAs and both decrease accuracy in invalid trials and increase accuracy in valid trials. Additional experiments should allow further understanding of these processes.

The present study gathered evidence that rats, similarly to human beings, exhibit an exogenous process of attention orienting detectable by way of both reaction times and accuracy for SOAs as short as 200 ms, and an endogenous process of attention orienting detectable by way of reaction time for longer SOAs and by way of accuracy for shorter SOAs. Bowman et al. (1993) showed that monkeys are capable of orienting endogenous attention toward the cued location when symbolic (central) cues validly indicate it; validity effects were observed for SOAs as short as 100 ms. It is not clear whether these results reflect either species differences relative to humans or the extensive training required by animals to achieve the level of performance required for testing in this kind of behavioral task. Rats also require extensive training to achieve performance levels adequate for testing in the covert attention paradigm. Thus, it is possible that orienting of endogenous attention in these animals, similarly to monkeys, becomes faster because of extensive training. More studies are required to evaluate this possibility.

The present study showed that rats trained in a task analogous to the covert attention task for humans with peripheral cues exhibited significant differences in reaction times and response accuracy when training involved predictive conditions compared with non-predictive conditions. While predictive valid cues reduced the proportion of omission errors, predictive invalid cues increased omission errors. In addition, the validity effects for reaction times were greater in the predictive condition. These results are congruent with those usually reported for humans, leading to the proposal that rats are capable of orienting visual attention in a way analogous to the endogenous orientation of attention by humans. Therefore, as employed in the present study, this behavioral task may prove useful for investigations involving both exogenous and endogenous processes of visual attention in rats.

Acknowledgments The authors thank three anonymous reviewers and Dr. Bárbara K.A. Onishi for criticisms and comments that helped to improve an early version of the present study. This research was supported by grants from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Coordenação de Aperfeiçoamento de Pessoal do Ensino Superior (CAPES), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brazil.

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