



Pupil dilation in response preparation

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Abstract

This study examined changes in pupil size during response preparation in a finger-cuing task. Based on the Grouping Model of finger preparation [Adam, J.J., Hommel, B. and Umiltà, C., 2003b. Preparing for perception and action (I): the role of grouping in the response-cuing paradigm. *Cognitive Psychology*. 46, (3), 302–358.; Adam, J.J., Hommel, B. and Umiltà, C., 2005. Preparing for perception and action (II) Automatic and effortful Processes in Response cuing. *Visual Cognition*. 12, (8), 1444–1473.], it was hypothesized that the selection and preparation of more difficult response sets would be accompanied by larger pupillary dilations. The results supported this prediction, thereby extending the validity of pupil size as a measure of cognitive load to the domain of response preparation.

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1. Introduction

Preparing to act facilitates motor performance. The underlying processes of this performance enhancement have been studied by means of response-cuing paradigms, in which cues provide information about some, or all, of the required response parameters before the actual target stimulus appears. Thus, cues in response-cuing paradigms allow and induce a process of response preparation that facilitates motor performance. For instance, in the finger-cuing paradigm developed by Miller (1982), a visual cue signal indicates a subset of two possible finger (i.e., key press) responses out of a total of four, thus allowing the selection and preparation of a subset of finger responses. The robust finding from this paradigm is that, given sufficient preparation time, informative cues substantially shorten reaction time (RT) relative to an uncued condition (Reeve and Proctor, 1990; Adam et al., 2003b). The present study extends the numerous chronometric studies on response preparation by examining its effect on a psychophysiological

measure, pupil dilation, with the purpose of further delineating its underlying mechanisms.

The cognitive pupillary response or the task-related change in pupil size has been shown to be a reliable measure of processing load and resource allocation, with larger pupil dilation reflecting greater processing load or mental effort. This has been established in many studies of language processing, perception, memory, complex reasoning, and attention, which all reported larger pupil dilations for more difficult tasks (Andreassi, 2000; Beatty and Lucero-Wagoner, 2000; Jennings and Van der Molen, 2005). In the present study, we used the sensitivity of the pupillary response to task complexity to test a theoretical account (Adam et al., 2003b, 2005) of an interesting phenomenon typically observed in the finger-cuing task, namely a pattern of differential preparation benefits. Before explaining this phenomenon and the proposed account, we first describe the finger-cuing task in detail.

In the finger-cuing task (Miller, 1982), participants are forewarned by a visual cue signal about a particular subset of possible finger responses. Typically, they respond to horizontally arranged stimuli by spatially compatible key press responses with the index and middle fingers of both hands placed

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adjacently. In the present study, the visual display consists of four white boxes on a computer monitor, in which the cue and target signals were presented (see Fig. 1). At the start of a trial, a neutral warning stimulus (“+” sign) appeared between the two center boxes for 1 s. Then, the cue signal was presented for 2 s by coloring two boxes grey. Following the cue signal, the target stimulus was presented by making one of the two grey boxes black, thus indicating the required finger response. The 2-s time interval between onset of the cue and onset of the target stimulus is called the preparation interval, as it reflects the amount of time participants have to selectively prepare the two finger responses indicated by the cue before the appearance of the target. The functional significance of the cue is that it transforms the basic four-choice task into a two-choice task. Four cue or preparation conditions can be distinguished (Fig. 1). In the *hand-cued* condition, the cue specifies two fingers on the same hand (e.g., the left-middle and left-index fingers). In the *finger-cued* condition, the cue specifies the same finger on two hands (e.g., the left-index and right-index fingers). In the *neither-cued* condition, the cue specifies different fingers on two hands (e.g., the left-index and right-middle fingers). These three preparation conditions are called the “cued” conditions. Also, an *uncued* control condition is included. Here, the cue does not provide advance information about the upcoming response (all four boxes turn grey), thus precluding selective response preparation. In other words, the uncued condition leaves the basic 4-choice task unaltered and, thus, is a control or baseline condition, against which the effects of the “cued” conditions can be evaluated. Since RTs in a 2-choice task are substantially shorter than RTs in a 4-choice task (Hick, 1952; Hyman, 1953), cue effectiveness is inferred from a significant RT advantage or benefit for the 2-choice “cued” conditions (i.e., hand-cued, finger-cued, and neither-cued) over the control, 4-choice (uncued) condition. Thus, with longer preparation intervals (1000 ms and more), hand-cued, finger-cued, and neither-cued conditions all show substantially shorter RTs than the uncued condition, reflecting the operation of selective preparation.

A strong and often replicated observation in the finger-cuing paradigm is a pattern of differential cuing benefits: RTs are shortest for the hand-cued condition, longest for the neither-cued condition, and intermediate for the finger-cued condition, suggesting an ordering in terms of preparation difficulty (Reeve and Proctor, 1990; Adam et al., 2003b). It should be noted,

however, that this pattern of differential cuing benefits only emerges with short preparation intervals (i.e., intervals less than about 1.5 s). When the preparation interval is extended to 2 s or more, the three cued conditions often show comparable RTs. Thus, certain pairs of responses can be selected and prepared more quickly than others, with small or no differences between the pairs given sufficiently long preparation time.

A recent account of the pattern of differential cuing benefits is the Grouping Model (Adam et al., 2003b, 2005), which is an extension of the salient-features coding principle (Reeve and Proctor, 1990). The key idea of the Grouping Model is that the individual elements of multi-element visual displays and multi-element response arrays are not processed independently but are preattentively organized or “grouped” according to low-level grouping factors that may depend on stimulus-driven (e.g., Gestalt principles) and response-related factors (e.g., inter-response dependencies). Thus, when presented with an array of four horizontally aligned potential target locations (centered on a person’s midline), left-right (i.e., hand-) cues are easily encoded into left or right visual groups based on the Gestalt principle of proximity. In addition, such left-right cues are also easily encoded into left-right response groups, which involve the two fingers on the left or right hands. No other set of cues affords such simple, strong perceptual–motor subgroups, as both inner-outer (i.e., finger-) cues and alternate (i.e., neither) cues require binding separate items across the midline. The outcome of this is that left-right or hand-cues can activate responses in a fast, bottom-up manner while the other cues must activate responses in a slower, top-down manner. Left-right cues may also cause automatic shifts of attention to the cued locations while bilateral cues may require volitional shifts of attention (Adam et al., 2003a, 2005). Together, these perceptual, motor, and attentional factors produce the left-right or hand-cued advantage.

There are now several experiments that support the Grouping Model. For example, the advantage of left-right or hand-cues can be reduced, and even eliminated, if the distance between the two inner cues is greatly reduced (i.e., making the inner cues the easiest to encode) (e.g., Adam et al., 2003a, Experiment 2; Reeve et al., 1992, Experiment 2) or if the four responses are mapped onto a single hand (i.e., eliminating the response grouping present with two fingers on two hands) (e.g., Adam et al., 2003a; Proctor and Reeve, 1986). Additionally, no-onset

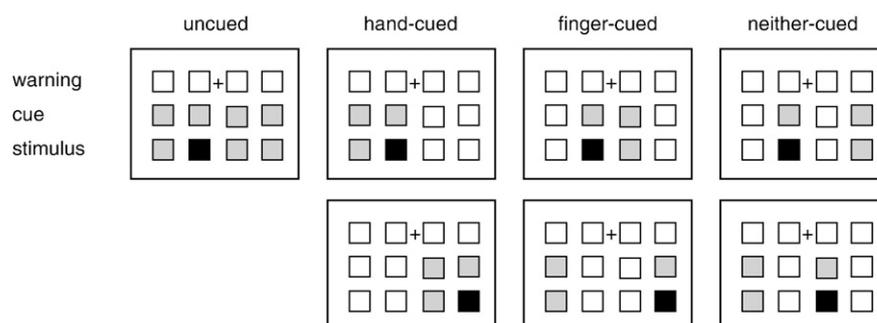


Fig. 1. A schematic representation of the finger-cuing task. Cue and target stimuli are presented overlaid and not in separate rows.

cues do not yield a hand-cued advantage, as the lack of an abrupt onset does not capture attention at the (left-right) cued locations (Adam et al., 2005, Experiment 1).

In sum, according to the Grouping Model, the processing advantage of the hand-cued condition simply reflects the natural and stronger grouping of the two leftmost and two rightmost elements in both the stimulus and response sets. That is, each stimulus set and each response set has a default organization established preattentively by the bottom-up computation of perceptual and motor units or subgroups. This process is fast and automatic. With additional, top-down processing, however, alternative organizations can be attained. This process is slow and effortful. Thus, the pattern of precuing effects that emerges in the finger-cuing task critically depends on the nature of these default groupings and on the time available to reorganize these representations, if necessary.

According to the Grouping Model, finger- and neither-cues are the more difficult cues because they require slow, effortful, top-down processing to break up the default, left-right spatial organization and to create a new perceptual and motor organization based on the characteristics of the cue. Furthermore, in this view, the neither-cued condition is more difficult than the finger-cued condition, because the former represents a perceptually asymmetrical subgroup that indicates the selection and preparation of two different, non-homologous fingers on two hands, whereas the latter represents a perceptually symmetrical subgroup that specifies the same or homologous fingers on two hands. Because homologous fingers are neurally and functionally linked (Rosenbaum, 1991), they are easier to group than non-homologous fingers.

Assumptions about good grouping are corroborated by independent evidence. For instance, the strong grouping of left and right perceptual subgroups is bolstered by research showing that people spontaneously and naturally divide the visual space into left-side and right-side parts (e.g., Mapp and Ono, 1999; Nicoletti and Umiltà, 1989). The stronger grouping of fingers on one hand as opposed to fingers on different hands is substantiated by the fact that cerebral control of hand and finger movements is almost completely localized in the contralateral frontal lobe (e.g., Hellige, 1993).

Additional support for the Grouping Model comes from an aging study, which showed that older age does not affect the RT benefits associated with hand-cues, but does strongly reduce the efficiency of the finger- and neither-cues, at least with preparation intervals equal or shorter than 2 s (Adam et al., 1998). Given that advancing age is accompanied by a reduction in central resources (Allen et al., 1993), while leaving automatic processes intact (Hasher and Zacks, 1979), this finding accords with the idea that hand-cues prompt the fast, bottom-up selection and preparation of fingers, whereas the more difficult finger- and neither-cues require slow and effortful top-down processes to establish a selective preparatory set.

The aim of the present study was to examine the effects of different response cues in the finger-cuing task on pupil dilation to provide a further test of the Grouping Model. The logic of the study was straightforward: If the pattern of differential cuing benefits in the finger-cuing task is associated with differences in

processing load or mental effort, with more difficult cues requiring more effortful processing, the largest pupillary dilation should be observed in the neither-cued condition, the smallest in the hand-cued condition, and an intermediate level of pupillary dilation in the finger-cued condition. Because we used a rather long preparation interval of 2 s (to allow sufficient time for the pupil to react), we expected all informative cue conditions (hand-, finger-, and neither-cues) to generate substantial RT benefits relative to the uncued condition. Importantly, however, the underlying preparatory processes that generated these benefits are expected to be different in terms of the involved processing load, and thus to be reflected in the pupillary response.

2. Method

2.1. Subjects

The experiment was carried out with 18 right-handed health-science, medicine, and psychology students from Maastricht University (9 women, 9 men; mean age = 22.7 years, $SD = 2.52$). All had normal or corrected-to-normal vision. None of them took eye medication that could influence pupil responses. Informed consent was obtained and they received €7.50 for their participation.

2.2. Stimuli and apparatus

The visual display consisted of a row of four white boxes (1 cm × 1 cm) in black outline, presented on a standard computer screen with a grey background, which corresponded to the calibration background. All four boxes were separated by 0.5 cm. Subjects were seated in a height-adjustable chair with their heads stabilized in a chinrest placed at a distance of 57 cm from the monitor. Subjects placed the index and middle fingers of both hands on four linearly arrayed push buttons mounted on a response box, placed in front of the subjects on a table, and aligned with the centre of the stimulus set. The illuminance in the room was constant (about 600 lx). RTs were measured in milliseconds. The software controlling the RT measurements and the stimulus presentation was programmed in Matlab 7 and supported by the Eyelink Toolbox (Brainard, 1997; Cornelissen et al., 2002). The pupil area was measured in pixels by the Eyelink I Gazetracker (SR Research Ltd., Canada), a head-mounted infrared video-based tracking system with a temporal resolution of 250 Hz and a spatial resolution of at least 0.01°.

2.3. Procedure

Each subject received a series of 80 test trials, preceded by 16 practice trials. Within the series of 80 test trials there were 20 trials for each cue condition (uncued, hand-cued, finger-cued, neither-cued) in a random order. Subjects were informed about the nature of the task and were explicitly told to take advantage of the informative cues. They were instructed to react as quickly as possible to the target stimulus by pressing the correct,

spatially corresponding, response key. No feedback was provided. At the start of each individual test session, a nine-point calibration and validation procedure was performed.

2.4. Data analysis

Trials with RTs of less than 125 ms or in excess of 1250 ms (1.46%) were considered outliers and were excluded from all data analyses. Mean RT and proportion of errors were calculated for each subject as a function of cue condition. Pupil data from the right eye were analyzed and only for correct trials (i.e., trials without response errors and RT outliers). Eye blinks were filtered out by a computer algorithm and area samples were replaced by cubic spline interpolation, starting 17 samples (i.e., 68 ms) before and ending 25 samples (i.e., 100 ms) after the blink.

For each trial, a baseline pupil area was determined by calculating the average pupil size during a period of 100 ms preceding the onset of the cue signal. Cue-locked pupil dilation was calculated by subtracting this baseline area from the pupil area for each data point during a period of 4 s following cue onset. This difference score was converted to a percentage of the corresponding baseline value. This conversion was warranted by Jin's (1992) revised version of the so-called Law of Initial Value (LIV), which states that within the middle range of baseline values, the physiological response increases as a function of baseline. This version of the LIV was applicable to our data, because there was a positive overall correlation between baseline pupil size and peak dilation ($r = .53$). The LIV introduces a physiological artifact, however, because it influences pupil dilation and thus may obscure the effect of cue condition. Expressing dilation as a percentage of the baseline corrects for this artifact, because pupillary responses following a relatively high baseline value are attenuated. This procedure was earlier applied by, for example, Van Gerven et al. (2004).

3. Results

3.1. Behavioral data

As expected, RTs in the three cued conditions were all substantially shorter ($M = 65$ ms) than those in the uncued condition ($M_s = 340$ ms, 325 ms, 335 ms, and 398 ms, for hand-cued, finger-cued, neither-cued, and uncued conditions, respectively). A one-way repeated-measures analysis of variance (ANOVA) on the RT data confirmed this picture by revealing a highly significant effect of cue condition, $F_{(3,51)} = 58.12$, $\eta^2 = .77$, $p < .001$. Tukey Least Significant Difference (LSD) post-hoc tests revealed large significant benefits for all three cued conditions relative to the uncued condition ($p_s < .001$), indicating that participants selectively prepared responses in all three cued conditions. Furthermore, the post-hoc tests revealed a small (i.e., 15 ms) but significant ($p < .05$) RT advantage for the finger-cued condition over the hand-cued condition. All other comparisons between the three cued conditions were not significant. Subjects made few errors, with a mean error rate of 1.5% ($M_s = 0.4\%$, 0.2%, 1.9%, and 3.8% for hand-cued, finger-cued, neither-cued, and uncued conditions, respectively). This number was too low for statistical analysis. Note, however, that the error rates mirror the RT time pattern, with fewer errors for the cued conditions than for the uncued condition, indicating that the cuing benefits were not due to a speed-accuracy trade-off.

3.2. Pupil data

Fig. 2 shows the mean pupil dilation (averaged over subjects) as a function of time (starting at cue onset until 3.5 s after cue onset) and cue condition (uncued, hand-cued, finger-cued, and neither-cued). This dilation-by-time plot reveals that the pupil started to dilate about 350 ms after cue onset, with thereafter a clear differentiation in the development of the dilation curves for the three cued conditions. Whereas the neither-cued

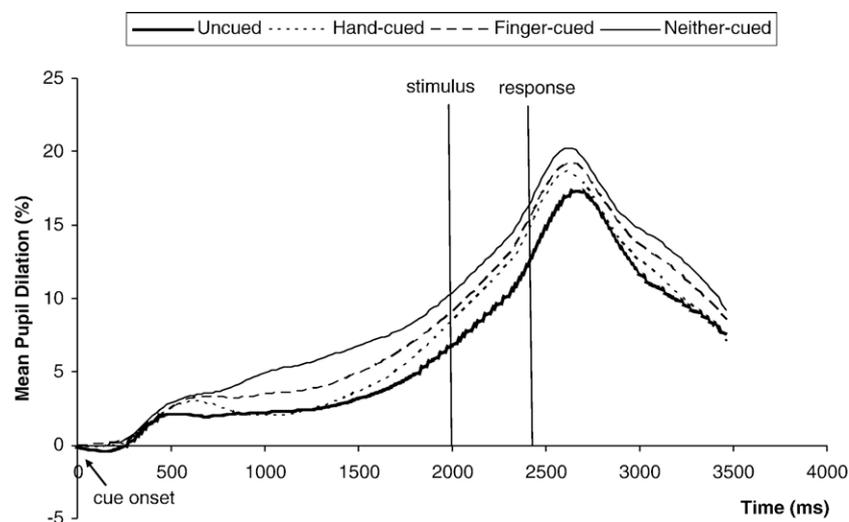


Fig. 2. A dilation-by-time plot for the four cue conditions starting from cue onset until 3.5 s afterwards. The stimulus is presented 2 s after cue onset and the response occurs on average 350 ms after stimulus onset.

condition showed a steady and continuous increase in pupil size throughout the preparation interval, the hand-cued condition tended to show a slight decrease midway through the preparation interval and a steady increase thereafter. The finger-cued condition showed an intermediate pattern, with a period of constant pupil size about halfway the preparation interval. From Fig. 2 it is clear that pupil dilation during the preparation interval is directly related to cue difficulty, with the neither-cued condition producing the largest pupil dilation, the hand-cued condition the smallest, and the finger-cued condition an intermediate dilation. A one-way repeated-measures ANOVA on the mean increase in pupil dilation as a function of cue condition (hand-cued, finger-cued, neither-cued, uncued) during the 500–2000 ms preparation interval (the interval that showed a differentiation between cue conditions), followed by Tukey LSD post-hoc tests, confirmed this picture by showing robust differences between all three cued conditions, $F_{(3,51)}=6.98$, $\eta^2=.291$, $p<.001$. This ordering of pupil dilation as a function of cue difficulty conforms to the predictions of the Grouping Model. Moreover, as can be seen in Fig. 2, overall, the uncued condition tended to produce the smallest increase in pupil size during the 500–2000 ms preparation interval, but its difference with the hand-cued condition was not statistically reliable ($p>.5$).

Finally, it is interesting to note that, after the preparation interval, the pupil continued to dilate strongly until some time after response execution (with a similar ordering, but less divergence, of cue conditions). This phenomenon has been observed before in a simple (1-choice) RT paradigm (Richer et al., 1983), and suggests that motor processes concerned with response execution and response monitoring carry a high cognitive load (Jennings and Van der Molen, 2005).

4. Discussion

The main outcome of this study was that difficulty of response preparation was reflected by pupil dilation. Difficulty of response preparation was manipulated by cuing two fingers on one hand (hand-cued), two homologous fingers on two hands (finger-cued), and two non-homologous fingers on two hands (neither-cued). Previous research has shown that these cuing conditions differ in cuing efficiency, with hand-cues being most efficient and neither-cues being least efficient. According to the Grouping Model (Adam et al., 2003b, 2005), this pattern of differential cuing benefits is due to differences in subgroup strength, with strong or natural subgroups requiring less cognitive effort to establish and prepare than weak or ambiguous subgroups. The present finding that larger pupillary dilations were observed for the selection and preparation of more difficult response sets provides converging evidence for the Grouping Model. Moreover, this finding is consistent with the results of a recent fMRI study, which showed greater levels of brain activity for the more difficult response cues in the finger-cuing paradigm, particularly in the parietal cortex (Adam et al., 2003a).

An additional finding was that during the preparation interval, pupil dilation in the hand-cued condition was not significantly different from that in the uncued condition, even though RTs in

the hand-cued condition were 58 ms shorter than those in the uncued condition. This outcome suggests that the preparatory process involved in hand-cues may indeed have occurred in a bottom-up, rather effortless way, which is distinct from the more effortful, top-down preparation of finger- and neither-cues. This outcome, as well as the finding that the RTs of the three cued conditions were similar but their pupil responses were not, indicates a dissociation between behavioral and psychophysiological measures of response preparation, as has been observed before (Miller et al., 1996; Jennings and Van der Molen, 2005). Furthermore, it advocates caution in assuming that task processing load can be estimated directly from RT measures. As Jennings and Van der Molen (2005) have emphasized, different indices of preparation correlate poorly and typically do not correlate highly with performance measures, suggesting that preparation is not a single process but rather a set of processes.

Another finding was that RT in the finger-cued condition was slightly (i.e., 15 ms) shorter than RT in the hand-cued condition. A similar finding has been reported before (albeit with a longer preparation interval of 3 s; Adam et al., 2003a, Exp.1) and can be attributed to the so-called Kornblum-effect, which is the phenomenon that standard 2-choice RTs are typically shorter with a between-hands response repertoire than with a within-hands repertoire, possibly because of less response competition in a between-hands set than in a within-hands set (Kornblum, 1965). This finding does not contradict the Grouping Model, because this model explicitly acknowledges the importance of the process of within-subgroup discrimination (which follows the process of subgroup making and selective preparation) as a determinant of RTs. When, according to the Grouping Model, long-duration cues have established “cleanly” defined two-choice response sets, there should be no advantage for hand-cues but rather an advantage for finger-cues (Adam et al., 2003a). How long the duration of the cues should exactly be to produce a finger-advantage depends on procedural factors (e.g., number and duration of the preparation intervals) and the spatial layout of the stimulus and response displays.

Differentiation of pupil dilation as a function of cue difficulty did not start until about 600–700 ms after onset of the cue. This relative late differentiation of the pupil response might be related to the fact that RT tasks require time-focused preparation (Jennings and Van der Molen, 2005). Participants do not want to start preparing too soon, because maintenance of preparation over longer time periods is difficult to sustain and experienced as aversive and effortful (e.g., Niemi and Näätänen, 1981). Hence, it is not surprising that participants show delayed pupil responses with long (e.g., 3 s) as compared to short (e.g., 1 s) preparation intervals (Richer et al., 1983). In this view, the present preparation interval of 2 s might be considered as relatively long. Indeed, previous research with the finger-cuing task has shown that optimal preparation benefits may be achieved within 1 s of preparation time (Adam et al., 1998).

We now consider several alternative explanations of the preparation advantage induced by left-right or hand-cues. A first alternative account of the hand advantage is the “spatial proximity” hypothesis. According to this hypothesis, preparation for two stimulus positions is more efficient the closer

together they are, possibly because of an advantage in sharing attention across nearby positions (Miller, 1982). This hypothesis, however, can be rejected because the observed effects do not support the explanation. That is, the spatial proximity hypothesis would predict shorter RTs when the two index fingers are cued than when the two middle fingers are cued, simply because the cue locations are in closer proximity in the former situation than in the latter. The results, however, do not support this prediction as RTs for preparing two middle or two index fingers were not significantly different ($p > .4$). Similar findings have been reported before (e.g., Adam, 1992; Miller, 1982).

A second alternative explanation is the “dark region” hypothesis. According to this account, the visual spatial cues differ in terms of the extend and dispersion of the local dark regions they occupy on the screen, with hand-cues having a big dark mass on the left or right side of the display and the other cues having dark spots on both sides of the center. This account, however, does not fit with the observation that pupil dilation in the hand-cued and uncued conditions was similar during the preparation interval, even though they differed in terms of physical appearance and darkness (illuminance).

The third alternative account focuses on the left-right distinction in the stimulus-response displays as being critical, with the hand-distinction being of no importance (e.g., Reeve and Proctor, 1984, 1990). From this perspective, the “hand”-advantage is due to the saliency of left-right spatial locations in the stimulus and response displays, with the specific effectors (fingers) assigned to these locations being of no or minor relevance. Using an overlapped placement of hands procedure (i.e., fingers of both hands alternating on response keys in the order: right index, left middle, right middle, left index), Reeve and Proctor (1984) reported that the usual advantage for the hand-cued condition (two fingers on one hand) turned into an advantage for the neither-cued condition (two fingers on different hands). On the basis of this finding, Reeve and Proctor (1984) argued that hand-cued advantage really is an advantage for the two leftmost and two rightmost stimulus-response locations, not for the left or right hand per se. Adam et al. (2003b), however, noticed that Reeve and Proctor’s result with the hand-placement manipulation might be restricted to, and thus an artifact of, two procedural factors: The task instructions provided to participants regarding the possibilities of preparation and the presentation mode of the preparation intervals. In particular, Adam et al. (2003b) observed that Reeve and Proctor (1984) did not explicitly instruct their participants to prepare all possible finger pairings, nor did they group the different preparation intervals together in separate blocks of trials. According to Adam et al. (2003b), this procedure might have favored the more natural left-right cues. Moreover, when Adam et al. (2003b, Experiment 5) investigated the hand-placement manipulation with more “optimal” preparation procedures (i.e., explicitly telling the participants to prepare all possible finger pairings, and grouping the different preparation intervals together in separate blocks of trials), they found that the advantage of the left-right cues disappeared. Thus, when the perceptually salient left-right cues are not combined with the anatomically based hand distinction, Reeve and Proctor’s “left-right” advantage disap-

pears. Therefore, it appears that the anatomically based hand distinction is a prerequisite for the left-right advantage to materialize and, hence, in effect can be considered a true hand advantage.

The Grouping Model’s bottom-up/top-down and automatic/effortful processing distinction is consistent with several modern dual-route conceptions of response selection (Kornblum et al., 1990). According to these views, response selection can occur via (a) a slow, indirect, translation route that applies a translation rule and draws upon central resources, and/or (b) a fast, direct, automatic response activation route that exploits natural and coherent stimulus-response links. Also, the Grouping Model is consistent with a recent, thorough review of the response preparation literature by Jennings and Van der Molen (2005), who identified several key features of response preparation, including its effortful and cognitive nature and its dependence on the complexity of the motor task. The present findings reinforce this framework and indicate that physiological changes during response preparation as indexed by changes in pupil size can be used to test a theory of response preparation.

Finally, it is relevant to note that the present study is not the first to examine pupillary responses during preparation for speeded action. However, whereas previous studies typically used a simple RT time paradigm (one target stimulus, one pre-specified response) and focused on the effects of stimulus uncertainty (e.g., Bradshaw, 1968; Richer et al., 1983; Jennings et al., 1998; Bitsios et al., 2004), the present study used a four-choice RT task and focused on the effects of response uncertainty. The consistent finding across all these studies is that greater uncertainty is associated with a reduced pupillary response, and that anticipation of the stimulus event and advance selection of the appropriate response both lead to an increased pupillary response. Hence, our study extends previous work that used the pupillary response as an index of processing load by showing that it is also sensitive to manipulations of task difficulty in the domain of response preparation.

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References

- Adam, J.J., 1992. The spatial proximity hypothesis of the hand advantage in spatial precuing tasks. *Hum. Mov. Sci.* 11, 641–652.
- Adam, J.J., Backes, W., Rijcken, J., Hofman, P., Kuipers, H., Jolles, J., 2003a. Rapid visuomotor preparation in the human brain: a functional MRI study. *Cogn. Brain. Res.* 16 (1), 1–10.
- Adam, J.J., Hommel, B., Umiltà, C., 2003b. Preparing for perception and action (I): the role of grouping in the response-cuing paradigm. *Cogn. Psychol.* 46 (3), 302–358.
- Adam, J.J., Hommel, B., Umiltà, C., 2005. Preparing for perception and action (II) Automatic and effortful Processes in Response cuing. *Vis. Cogn.* 12 (8), 1444–1473.
- Adam, J.J., Paas, F.G.W.C., Teeken, J.C., van Loon, E.M., van Boxtel, M.P., Houx, P.J., Jolles, J., 1998. Effects of age on performance in a finger-precuing task. *J. Exp. Psychol. Hum. Percept. Perform.* 24 (3), 870–883.

- Allen, P.A., Groth, K.E., Weber, T.A., Madden, D.J., 1993. Influence of response selection and noise similarity on age differences in the redundancy gain. *J. Gerontol.* 48 (4), P189–P198.
- Andreassi, J.L., 2000. Pupillary response and behaviour. In: Mahwah, N.L.E.A. (Ed.), *Psychophysiology. Human behav. Physiol. response*, Vol. 10. Oxford University Press, New York, pp. 218–233.
- Beatty, J., Lucero-Wagoner, B., 2000. The pupillary system. In: Cacioppo, J.T., Tassinary, L.G., Berntson, G.B. (Eds.), *Handbook of Psychophysiology*. Cambridge University Press, Cambridge, pp. 142–162.
- Bitsios, P., Szabadi, E., Bradshaw, C.M., 2004. The fear-inhibited light reflex: importance of the anticipation of an aversive event. *Int. J. Psychophysiol.* 52 (1), 87–95.
- Bradshaw, J.L., 1968. Pupillary changes and reaction time with varied stimulus uncertainty. *Psychon. Sci.* 13 (2), 69–70.
- Brainard, D.H., 1997. The Psychophysics Toolbox. *Spat. Vis.* 10 (4), 433–436.
- Cornelissen, F.W., Peters, E.M., Palmer, J., 2002. The EyeLink Toolbox: eye tracking with MATLAB and the Psychophysics Toolbox. *Behav. Res. Meth. Instrum. Comput.* 34 (4), 613–617.
- Hasher, L., Zacks, R.T., 1979. Automatic and effortful processes in memory. *J. Exp. Psychol.* 108, 356–388.
- Hellige, J.B., 1993. *Hemispheric asymmetry: what's right and what's left*. Harvard University Press, Cambridge, Massachusetts.
- Hick, W.E., 1952. On the rate of gain of information. *Q. J. Exp. Psychol.* 4, 11–26.
- Hyman, R., 1953. Stimulus information as a determinant of reaction time. *J. Exp. Psychol.* 45 (3), 188–196.
- Jennings, J.R., Van der Molen, M.W., 2005. Preparation for speeded action as a psychophysiological concept. *Psychol. Bull.* 131 (3), 434–459.
- Jennings, J.R., Van der Molen, M.W., Steinhauer, S.R., 1998. Preparing the heart, eye, and brain: foreperiod length effects in a nonaging paradigm. *Psychophysiology* 35 (1), 90–98.
- Jin, P., 1992. Toward a reconceptualization of the law of initial value. *Psychol. Bull.* 111 (1), 176–184.
- Kornblum, S., 1965. Response competition and/or inhibition in two-choice reaction time. *Psychon. Sci.* 2, 55–56.
- Kornblum, S., Hasbroucq, T., Osman, A., 1990. Dimensional overlap: cognitive basis for stimulus-response compatibility—a model and taxonomy. *Psychol. Rev.* 97 (2), 253–270.
- Mapp, A.P., Ono, H., 1999. Wondering about the wandering cyclopean eye. *Vision Res.* 39 (14), 2381–2386.
- Miller, J., 1982. Discrete versus continuous stage models of human information processing: in search of partial output. *J. Exp. Psychol. Hum. Percept. Perform.* 8 (2), 273–296.
- Miller, J., Coles, M.G., Chakraborty, S., 1996. Dissociation between behavioral and psychophysiological measures of response preparation. *Acta Psychol.* 94 (2), 189–208 (Amst).
- Nicoletti, R., Umiltà, C., 1989. Splitting visual space with attention. *J. Exp. Psychol. Hum. Percept. Perform.* 15 (1), 164–169.
- Niemi, P., Näätänen, R., 1981. Foreperiod and simple reaction time. *Psychol. Bull.* 89, 133–162.
- Proctor, R.W., Reeve, T.G., 1986. A caution regarding use of the hint procedure to determine whether partial stimulus information activates responses. *Percept. Psychophys.* 40 (2), 110–118.
- Reeve, T.G., Proctor, R.W., 1984. On the advance preparation of discrete finger responses. *J. Exp. Psychol. Hum. Percept. Perform.* 10 (4), 541–553.
- Reeve, T.G., Proctor, R.W., 1990. The salient-features coding principle for spatial- and symbolic-compatibility effects. In: Proctor, R.W., Reeve, T.G. (Eds.), *Stimulus-response compatibility*. North-Holland, Amsterdam, pp. 163–180.
- Reeve, T.G., Proctor, R.W., Weeks, D.J., Dornier, L., 1992. Saliency of stimulus and response features in choice-reaction tasks. *Percept. Psychophys.* 52 (4), 453–460.
- Richer, F., Silverman, C., Beatty, J., 1983. Response selection and initiation in speeded reactions: a pupillometric analysis. *J. Exp. Psychol. Hum. Percept. Perform.* 9 (3), 360–370.
- Rosenbaum, D.A., 1991. *Human Motor Control*. Academic Press, New York.
- Van Gerven, P.W.M., Paas, F., Van Merriënboer, J.J.G., Schmidt, H.G., 2004. Memory load and the cognitive pupillary response in aging. *Psychophysiology* 41 (2), 167–174.